



Consequences of maternal loss before and after weaning in male and female wild chimpanzees

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Abstract

The mother-offspring relationship is paramount in most mammals and infant survival often depends on maternal investment. In species with prolonged periods of development or co-residence, mothers may continue to influence their offspring's outcomes beyond nutritional independence with benefits biased towards the philopatric sex. Chimpanzees (*Pan troglodytes*) are long-lived mammals with a protracted period of immaturity during which offspring continue to travel with their mothers. In contrast to most mammals, chimpanzees are also typically male philopatric. Here, we use over 50 years of demographic data from two communities in Gombe National Park, Tanzania, to examine the survival and longevity of both male and female chimpanzees that experienced maternal loss during three different age categories. Males who were orphaned between the ages of 0–4.99 years, 5–9.99 years, and 10–14.99 years all faced significantly lower survival than non-orphans and died earlier than expected. Females faced similarly reduced survival probabilities when orphaned between 0–4.99 and 5–9.99 years of age; however, females who experienced maternal loss between 10 and 14.99 years of age were no more likely to die than non-orphans. Females orphaned in this later age class also lived significantly longer beyond maternal loss than their male counterparts. As observed in other mammals, philopatric male chimpanzees may continue to benefit from their mother's ecological knowledge, whereas maternal influence on female offspring likely fades as they prepare to emigrate. These results emphasize how maternal influence on offspring outcomes can extend well beyond weaning, particularly for the philopatric sex.

Significance statement

Mammalian mothers are crucial to their infant's survival and in species where offspring continue to live with their mothers after weaning, maternal influence may extend beyond dependence on mother's milk. While in most group-living mammals females remain in their natal group, chimpanzees typically display the opposite pattern with males residing alongside their mothers into adulthood. Using over 50 years of data on wild chimpanzees, we investigated the consequences of maternal loss both before and after weaning. We found that both males and females orphaned up to 10 years of age were less likely to survive than non-orphans; however, only males orphaned between 10 and 15 years also faced lower survival. These results emphasize how chimpanzee mothers continue to matter for offspring beyond infancy and provide novel data on reduced maternal influence on survival for daughters compared to sons.

Keywords Maternal absence · Orphan · Survival · Female dispersal

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Introduction

Mammalian mothers are of primary importance for their offspring's development, not only as the main source of nutrition during gestation and lactation, but also as the chief provider of transportation, protection, and social support, as well as a model for social learning (reviewed in Clutton-Brock 1991; Nowak et al. 2000; Maestriperi and Mateo 2009; Lonsdorf 2012). Across taxa, non-mutually exclusive factors such as maternal condition, ecological knowledge, social position, and behavior all contribute to offspring outcomes. In group-living species, the mother-offspring relationship also provides young mammals with a crucial social bond, as well as a substrate on which to build social skills and a pathway for integration into the broader social network (Altmann 1980; East et al. 2009; Maestriperi and Mateo 2009). These maternal contributions are particularly pronounced in social species that exhibit prolonged periods of development or in which mothers and offspring continue to reside together post-weaning (Fairbanks 2000; van Noordwijk 2012; Maestriperi 2018).

Any disruption of this mother-offspring relationship either before or after nutritional independence can have a number of adverse consequences in terms of physical and behavioral development. For example, in captive infant macaques (*Macaca mulatta*), maternal loss through social deprivation was associated with several negative behavioral consequences during adulthood, such as abnormal aggressive, social, and sexual behavior (e.g., Harlow et al. 1965; Suomi 1997). Maternal loss in ungulates is associated with markers indicative of poor physical condition, such as lower probability of antler growth in red deer (*Cervus elaphus*) orphaned before weaning (Andres et al. 2013) and weight loss in reindeer (*Rangifer tarandus*) orphaned after weaning (Holand et al. 2012). More recently, research on wild African elephants (*Loxodonta africana*) revealed that females orphaned after the typical weaning age associated less with higher-ranking individuals, received more aggression, were often found on the periphery of the group, and were the only females observed to emigrate from their natal group (Goldenberg and Wittemyer 2017, 2018).

Indeed, there is a growing body of literature documenting the continued influence of mammalian mothers on offspring outcomes well beyond nutritional independence (e.g., Watts et al. 2009; Foster et al. 2012; van Noordwijk 2012; Andres et al. 2013); however, the nature and degree of impact often depend on offspring sex and species-typical dispersal patterns. Most group-living mammalian species exhibit male-biased dispersal where males emigrate before reproducing while females remain in their natal group (Greenwood 1980); thus, mammalian mothers typically have an extended opportunity to influence female offspring outcomes. In matrilineal species such as spotted hyenas (*Crocuta crocuta*) and cercopithecine primates, mothers provide weaned and even fully independent

adult daughters with access to preferred resources and support during competitive interactions (spotted hyenas: Kruuk 1972; baboons [*Papio* spp.]: Cheney 1977; Lee and Oliver 1979; Altmann and Alberts 2005; vervet monkeys [*Chlorocebus pygerythrus*]: Horrocks and Hunte 1983). Mothers can also serve as repositories of social and ecological knowledge for the weaned offspring with whom they continue to associate. For example, post-reproductive female killer whales (*Orcinus orca*), who live in matrilineal-based groups, lead group movement in salmon foraging grounds during periods of low salmon abundance, with mothers more likely to lead sons than daughters (Brent et al. 2015). Similarly, Foley et al. (2008) suggested that older African elephant matriarchs with greater ecological knowledge were better able to lead their clans during a severe drought. Additionally, older female elephant matriarchs are better able to discriminate calls from non-group members than younger females and behave accordingly (McComb et al. 2001), potentially increasing reproductive success for their daughters (Lee et al. 2016).

In some species, maternal loss after weaning can have significant fitness consequences for the orphaned offspring. In the female philopatric red deer, orphaning both before and after weaning increased the risk of natural death for both sexes; however, the effect was stronger and more persistent for females than males (Andres et al. 2013). In spotted hyenas, another female philopatric species, female offspring that lost their mothers within 6 months of weaning had higher mortality than those whose mothers were present (Watts et al. 2009). Similarly, in female philopatric baboons, maternal loss before menarche was a source of early adversity that both alone and as part of a cumulative measure predicted lower probability of survival (Tung et al. 2016). Indeed, the adverse effects of maternal loss in baboons extend across generations as the offspring of females who experienced early maternal loss were less likely to survive than offspring of females who did not experience early maternal loss (Zipple et al. 2019). In killer whales, mothers continue to influence offspring fitness well into adulthood, as maternal death increased mortality risk in offspring themselves over 30 years of age (Foster et al. 2012). Interestingly, in this bisexually philopatric species where both sexes travel in matrilineal groups throughout their lifetimes, the effect was stronger for males than females.

As a social species with a prolonged period of post-weaning maternal association, chimpanzees (*Pan troglodytes*) are particularly likely to experience negative consequences of maternal loss. Wild chimpanzees live in multi-male, multi-female groups characterized by high fission-fusion dynamics in which the larger community of ~20–200 individuals form smaller subgroups that change in size and composition throughout the day (Nishida 1968; Goodall 1986). Within this fluid social system, chimpanzees form highly differentiated, individually specific relationships and engage in a suite of cooperative and competitive behaviors, including food

sharing, coalition formation during agonistic interactions, and territorial defense (Goodall 1986; Mitani 2009; Pusey and Schroepfer-Walker 2013). Chimpanzee offspring are typically weaned between the ages of 3–5 years (Clark 1977; Pusey 1983; van de Rijt-Plooij and Plooij 1987; Lonsdorf et al. 2019); however, after weaning, juvenile chimpanzees continue to travel with their mothers and younger siblings for an additional 4–5 years (Pusey 1983, 1990; Goodall 1986). As they mature, infant and juvenile chimpanzees must not only invest in somatic growth and developing adult dietary patterns and feeding behaviors (e.g., Matsumoto 2017; Bray et al. 2018), but also undergo the prolonged process of acquiring the social savvy to successfully navigate their complex social landscape (Pusey 1983, 1990; Goodall 1986; Lonsdorf and Ross 2012).

During their protracted period of immaturity, chimpanzee mothers remain an important social partner (Pusey 1983, 1990; Watts and Pusey 2002; Stanton et al. 2017) and behavioral differences between orphaned and non-orphaned chimpanzees have been reported to begin early and persist into adulthood. Goodall (1986) described anxiety and depressive behaviors such as listlessness, lethargy, rocking, hair pulling, and reduced play behavior in wild chimpanzees that lost their mothers during immaturity. A later study of the same population found that adolescent chimpanzee orphans exhibited higher levels of anxiety-related behaviors and reduced levels of play behavior compared to similarly aged individuals whose mothers were still alive (Botero et al. 2013). Conversely, juvenile orphans living in a sanctuary setting were observed to have higher levels of play behavior than non-orphans; however, orphan play bouts were shorter and more likely to result in aggression than those of mother-reared juveniles (van Leeuwen et al. 2013). Further research on captive populations suggests that these early differences may have lifelong consequences, as zoo-raised, maternally deprived chimpanzees exhibited reduced grooming activity and were less socially integrated in their grooming networks as adults compared to zoo-raised non-deprived chimpanzees (Kalcher-Sommersguter et al. 2015).

Unlike most mammals, female chimpanzees typically disperse at puberty while males remain in their natal community and reside alongside their mothers (Pusey 1979; Boesch and Boesch-Achermann 2000; Nishida et al. 2003; Kahlenberg et al. 2008; Langergraber et al. 2009). A recent study of maternal loss in the chimpanzees of Mahale Mountains National Park, Tanzania, revealed a significant post-weaning fitness benefit of maternal presence for sons. Nakamura et al. (2014) found that male offspring that lost their mothers between the ages of 0–3 years and 5–13 years, but not 13–16 years, faced significantly higher mortality risk than offspring that did not experience maternal loss and orphaned males died significantly earlier than expected. Data on female offspring outcomes in Mahale were limited since females

typically leave the study community during adolescence; however, a greater proportion of female orphans survived to age 9 years and the survival ratio for females who lost their mothers after 3 years of age did not differ between orphans and non-orphans. These results suggest that females do not face the same consequences of maternal loss as their male counterparts (Nakamura et al. 2014).

Here, we use almost 60 years of demographic data on two neighboring communities of eastern chimpanzees (*Pan troglodytes schweinfurthii*) in Gombe National Park, Tanzania, to investigate the consequences of maternal loss during immaturity (birth–15 years of age) in both males and females. The female-biased dispersal of chimpanzees leads to difficulties accumulating data on female offspring outcomes; however, ~50% of females born in the Kasekela community of Gombe National Park remain in their natal group (Pusey and Schroepfer-Walker 2013). Furthermore, when an adolescent female emigrates from one Gombe study community to the other, they are not lost to researchers. Thus, these data are uniquely suited to investigating potential sex differences in the consequences of maternal loss. Given nutritional dependence, we predict that any offspring orphaned at younger, typically pre-weaning, ages will have a significantly lower probability of survival than non-orphans. Furthermore, given the continued investment in weaned offspring by chimpanzee mothers and the results of Nakamura et al. (2014), we predict that orphaned offspring will have a significantly lower probability of survival and shorter lifespans than non-orphans; thus, this consequence will be present for individuals who experience maternal loss both pre- and post-weaning. However, since male philopatry is species-typical for chimpanzees, contrary to results from female or bisexually philopatric species (e.g., red deer: Andres et al. 2013; killer whales: Foster et al. 2012), we predict that the effect of maternal loss at later ages on survival will be reduced for females compared to males.

Methods

Study site and subjects

Gombe National Park is a ~35-km² strip of land on the eastern shore of Lake Tanganyika in western Tanzania and currently home to three chimpanzee communities: Kasekela, Mitumba, and Kalande. Here, we focus on demographic data from two habituated communities, Kasekela and Mitumba, which have been studied continuously since 1963 and 1985 respectively. Over the course of the study, the Kasekela community ranged from 38 to 64 individuals, while the Mitumba community ranged from 19 to 29 individuals.

Demographic data and samples

We used long-term demographic records based on observations of known individuals. Given the fission-fusion dynamics of wild chimpanzee communities, individuals are not necessarily seen every day. Birthdates are assigned based on the midpoint of the last day the mother was observed without an infant and the first day the mother was observed with an infant, with the exception of cases where there are signs of more recent birth, such as an attached umbilical cord (Strier et al. 2010). Individuals are assigned departure dates based on the last date on which they were observed and are considered dead if strong circumstantial evidence exists, such as observed poor health, or if their disappearance violates population-specific behavioral patterns (for further details see Strier et al. 2010). Individuals who departed without evidence of death or violations were categorized as permanently disappeared and right censored in demographic analyses (see below). Data were not recorded blindly as they are on focal animals in the field.

Given the observational nature of these data, certain demographic records have a higher degree of certainty than others. Thus, we fit four sets of models using samples that differed in inclusion criteria and, in a few cases, definition of an orphan. The larger, inclusive sample ($N = 247$; see Table 1) was comprised of all known sex individuals known or estimated to be immature (females: < 12 years of age and not yet experiencing full sexual swellings [Wallis 1997]; males: < 15 years of age [Goodall 1986]) when they entered the study (entry could be by the start of the study, by birth, or by immigration). Six females were excluded because they were known to be cycling when they first entered the study and were therefore not considered immature. We also ran analyses on a smaller sample restricted to known sex individuals whose birthdates were estimated within 90 days of certainty ($N = 193$; see Table 1). Eight offspring ($N_{\text{male}} = 3$; $N_{\text{female}} = 5$) included in both the inclusive and restricted samples were assigned the same death

date as their mothers. Since we cannot determine whether the offspring died at the same time/of the same cause as their mother, or as a result of their mother's death, we ran models in which these eight individuals were considered orphans and models in which the eight individuals were not considered orphans. Below, we present the results using both the inclusive and restricted samples where offspring with the same death date as their mothers are not considered orphans (which is a more conservative approach) (see supplemental materials (Online Resource 1) for results of models where those eight individuals were considered orphans).

Survival analyses

We examined the consequences of maternal loss on offspring survival using extended Cox proportional hazards models with age at maternal loss included as a time-varying covariate. Time-varying covariates in Cox models allow the value of a covariate to change over time. In this case, offspring were not considered orphans until after the age at which they experienced maternal loss (see Online Resource 2 for demographic data and ages at maternal loss). In order to investigate the influence at various ages, maternal loss was divided into three separate age categories that roughly correspond to infancy, i.e., individuals who are not weaned (0–4.99 years), juvenility, i.e., individuals who are weaned and have not yet gone through puberty (5–9.99 years), and adolescence/early adulthood (10–14.99 years). Individuals that disappeared (see above) and individuals alive as of January 31, 2019, were right censored. This approach of including each orphan age range as a separate effect, rather than a single effect of maternal loss, facilitates comparison of maternal loss in various age classes (see Online Resource 1 for model specification).

We modeled males and females separately given that chimpanzee males are often reported to have higher mortality than females during at least some period of their lifespans (e.g., Hill et al. 2001; Muller and Wrangham 2014; Wood et al. 2017); however, to test if one sex faced a greater risk of death following maternal loss than the other, we compared the hazards of death at each maternal loss category using Wald chi-square test statistics calculated as:

$$\frac{(b_1 - b_2)^2}{(se_{b_1})^2 + (se_{b_2})^2}$$

where b_1 and b_2 are estimates of β from male and female models respectively and se_{b_1} and se_{b_2} are their standard errors. If a calculated test statistic exceeded 3.87, the critical value for $\alpha = 0.05$ with 1 degree of freedom, then the two hazards were considered significantly different (Allison 2010; Andres et al. 2013).

Table 1 Sample sizes for number of offspring in each maternal loss category in each sample

Maternal loss category	Inclusive sample		Restricted sample	
	Males	Females	Males	Females
Orphaned 0–4.99 ^a	8	8	6	6
Orphaned 5–9.99 ^b	13	20	9	8
Orphaned 10–14.99	11	8	5	2
Not orphaned 0–14.99	97	82	85	72
Total	129	118	105	88

^a Three males and four females with same depart date as their mother before age 5 are not considered orphans and counted as Not orphaned

^b One female with same depart date as mother between ages 5 and 9.99 years is not considered an orphan and counted as Not orphaned

Life expectancy

We further examined the longevity of orphans in the inclusive sample by examining life expectancy at the time of maternal loss. Life expectancies at each year of life (i.e., years of life remaining for individuals still alive at the start of each age year) for each sex were obtained from recently published Gombe chimpanzee life tables (Bronikowski et al. 2016). We then calculated the expected age of death (age at maternal loss + life expectancy) for each orphan and, for those individuals with known death dates, compared expected ages at death to observed ages at death using non-parametric Wilcoxon signed-rank tests. Furthermore, we investigated potential sex differences in the lifespan of orphans. Specifically, we used non-parametric permutation tests (10,000 iterations) to compare the number of years male versus female orphans lived following maternal loss in each age category. A Bonferroni correction for multiple comparisons was applied to the results of the permutation tests. All statistical analyses were conducted in R v. 3.6.0 (R Core Team 2019) using the survival package for Cox models (Therneau 2015) and the coin package for permutation tests (Hothorn et al. 2008).

Results

Survival analysis

In the inclusive sample of males, non-orphan survival probabilities were 0.692 at 5 years of age, 0.598 at 10 years of age, and 0.534 at 15 years of age. Maternal loss in all three age categories was associated with significantly lower survival (Table 2; Fig. 1a). For females, non-orphan survival probabilities were 0.733 at 5 years of age, 0.686 at 10 years of age, and 0.663 at 15 years of age. However, in females only, maternal loss between the ages of 0–4.99 years and 5–9.99 years was associated with significantly lower survival; maternal loss between the ages of 10–14.99 years was not a significant predictor of survival (Table 2; Fig. 1b). There were no significant sex differences in hazard of death following maternal loss in any of the three age categories (0–4.99: Wald $X^2 = 0.427$, $p > 0.05$; 5–9.99: Wald $X^2 = 0.274$, $p > 0.05$; 10–14.99: Wald $X^2 = 1.809$, $p > 0.05$).

Table 2 Results of separate Cox proportional hazards models examining the effects of maternal loss on survival of male and female chimpanzees at various age categories. Results are from models fitted using the inclusive dataset

Maternal loss age category	Males				Females			
	β	HR	SE (β)	<i>p</i>	β	HR	SE (β)	<i>p</i>
0–4.99 years	0.988	2.687	0.439	<i>0.024</i>	1.467	4.335	0.570	<i>0.010</i>
5–9.99 years	1.140	3.128	0.387	<i>0.003</i>	1.485	4.415	0.511	<i>0.004</i>
10–14.99 years	1.486	4.420	0.464	<i>0.001</i>	0.285	1.330	0.753	0.705

Significance ($p < 0.05$) is indicated in italics

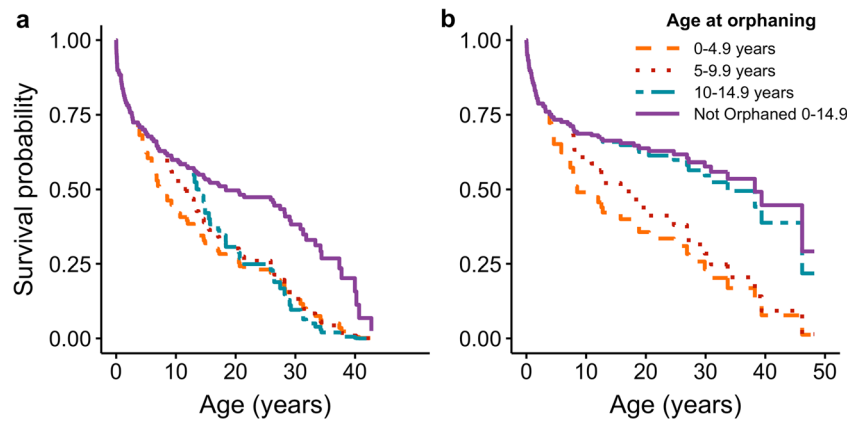
A similar pattern emerged in the restricted sample; however, for both sexes, only maternal loss in the earliest age class was significantly associated with lower survival (Table 3). Survival probabilities for non-orphaned males were 0.649 at 5 years of age, 0.555 at 10 years of age, and 0.479 at 15 years of age. Survival probabilities for non-orphaned females were 0.659, 0.601, and 0.579, respectively. Notably, in this more limited sample, there were only two females who lost their mothers between the ages of 10 and 14.99 years; thus, we were unable to include this age class in the model. There were no significant sex differences in hazard of death following maternal loss in either of the two age categories included in both models (0–4.99: Wald $X^2 = 2.101$, $p > 0.05$; 5–9.99: Wald $X^2 = 0.109$, $p > 0.05$).

Life expectancy

We compared observed and expected ages at death for 28 orphan males and 17 orphan females with known death dates in the inclusive sample. For males, the median difference between observed and expected age at death was –7.63 years (IQR = 15.61 years), which was statistically significant (Wilcoxon signed-rank test: $V = 75$, $p = 0.003$), indicating that male orphans died earlier than expected. For females, the median difference between observed and expected age at death was –13.66 years (IQR = 21.99 years), which was also statistically significant (Wilcoxon signed-rank test: $V = 27$, $p = 0.017$). However, there were seven female orphans, but no male orphans, who have lived beyond their expected age at death and are still alive. When these individuals are included in the analysis using their observed age at last census, the difference between observed and expected age of death is no longer significant for females (Med_{difference} = 3.34 years, IQR_{difference} = 23.08 years; $V = 132$, $p = 0.280$).

Non-parametric permutation tests revealed that there was a difference between the sexes in the number of years beyond maternal loss individuals lived only among those who lost their mothers between 10 and 14.99 years of age, with females living significantly longer than males (permutation test: 0–4.99: $N_{\text{male}} = 7$, $N_{\text{female}} = 5$, corrected $p = 0.999$; 5–9.99: $N_{\text{male}} = 12$, $N_{\text{female}} = 9$, corrected $p = 1$; 10–14.99: $N_{\text{male}} = 9$, $N_{\text{female}} = 3$, corrected $p = 0.015$; Fig. 2).

Fig. 1 Predicted survival curves from Cox proportional hazards models fit using the inclusive sample for **a** male and **b** female offspring who experienced maternal loss at each age category and those who did not experience maternal loss between ages 0–14.99 years



Discussion

As expected, maternal loss during immaturity has a negative effect on chimpanzee offspring survival when it occurs both before and after weaning. For male offspring, survival probability decreased whether they were orphaned between 0–4.99, 5–9.99, or 10–14.99 years of age. This result is mostly consistent with those reported by Nakamura et al. (2014) for Mahale male orphans where, using slightly different age categories, survival rates decreased for males who were orphaned at ages 0–5 and 5–13 years, but not those males orphaned between the ages of 13–16 years. Also consistent with results from Mahale, Gombe male orphans died significantly earlier than expected given the age at which they lost their mothers. Greater mortality risk in the youngest age category is not surprising as many of these orphans were likely still nutritionally dependent on their mothers. The youngest orphans to survive more than two years in Mahale were 37 months old (Nakamura and Hosaka 2015), while among the chimpanzees of Tai forest, Cote d’Ivoire, the earliest age at which an orphan survived was 30 months (Boesch et al. 2010). In this study, the youngest orphan to survive for longer than 2 years was 38.6 months old. However, the decreased survival probabilities of males orphaned from 5 to 14.99 years of age emphasize importance of mothers to sons past infancy.

In Nakamura et al. (2014), the limited knowledge of orphan female outcomes understandably prevented the use of standard survival analysis techniques; however, their results did suggest that females from infancy through emigration were less susceptible to increased mortality as a result of maternal

loss. Our results indicate that in Gombe, orphaned females face a similar increase in mortality risk to males until the oldest age category of 10–14.99 years. In the inclusive sample of Gombe females where all three age categories were represented, maternal loss was associated with decreased survival in the 0–4.99- and 5–9.99-year age categories and the estimated effect of maternal loss in these categories for females was not significantly different from males. However, Gombe females who lost their mothers between the ages of 10–14.99 years were no more likely to die than females whose mothers were present. Furthermore, females who lost their mothers at these later ages lived significantly longer post-orphaning compared to males. There was also no difference between the observed and expected age at death for female orphans from Gombe, further highlighting a sex difference in the consequences of maternal loss. Given that female dispersal is species typical in chimpanzees, it is unsurprising that older immature female orphans do not face the same survival consequences as males. Indeed, a study of female dispersal in the Kanyawara community of chimpanzees in Kibale, Uganda, found decreased association with mothers in the year preceding dispersal (Stumpf et al. 2009), which would limit the opportunity mothers have to influence their daughters’ survival outcomes even before they are permanently separated by emigration. This pattern regarding the potential for reduced maternal influence on survival appears to be conserved in Gombe where ~50% of Kasekela females remain in their natal community. Whether Gombe females who stay in their natal community have greater longevity in general compared to those

Table 3 Results of separate Cox proportional hazards models examining the effects of maternal loss on survival of male and female chimpanzees at various age categories. Results are from models fitted using the restricted dataset

Maternal loss age category	Males				Females			
	β	HR	SE (β)	<i>p</i>	β	HR	SE (β)	<i>p</i>
0–4.99 years	1.019	2.769	0.515	<i>0.048</i>	2.149	8.579	0.586	<i>< 0.001</i>
5–9.99 years	0.873	2.394	0.470	0.063	1.190	3.288	0.839	0.156
10–14.99 years	1.044	2.840	0.699	0.136	–	–	–	–

Significance ($p < 0.05$) is indicated in italics

who emigrate remains an open question to be answered as data on emigrants accumulate. Notably, evidence suggests that those females who do not emigrate from the Kasekela study community accrue benefits other than favorable survival outcomes. For example, natal females whose mothers are alive mature faster (Walker et al. 2018) and enter the adult dominance hierarchy higher (Foerster et al. 2016a) than those whose mothers are not alive and present in the community. Intriguingly, recent work at Gombe also suggests that maternal loss itself may influence whether females transfer, as females who have a mother present and high ranking in the community are less likely to disperse than females whose mothers are low-ranking or dead (Walker and Pusey *in press*).

The results of this study support previous research in chimpanzees (Nakamura et al. 2014) and other mammals (e.g., Watts et al. 2009; Foster et al. 2012; Andres et al. 2013) that document survival consequences of post-weaning maternal loss. However, the observed difference in survival between orphans and non-orphans raises the question of how independent chimpanzee offspring continue to benefit from maternal presence. As in killer whales (Brent et al. 2015), weaned chimpanzee offspring may benefit from the ecological knowledge of their mothers. Chimpanzees are considered ripe fruit specialists (Conklin-Brittain et al. 2001) and Gombe chimpanzees inhabit a spatially and temporally heterogeneous habitat (Pintea 2007; Foerster et al. 2016b). Adult males in the Kasekela community in Gombe concentrate their solitary space use to the same areas in which their mothers ranged during dependency, presumably providing males better knowledge of resource distribution (Murray et al. 2008). Maternal ecological knowledge may be particularly valuable for adolescent males who maintain a steep increase in mass until ~ 13 years of age, whereas the steep increase of mass in females ends at ~ 10 years of age (Pusey et al. 2005). In bonobos, the other species in the genus *Pan*, adult females are co-dominant with males and maternal presence is associated with greater mating success in sons (Surbeck et al. 2011, 2019). Conversely, chimpanzee males are dominant over all females and maternal presence is not associated with increased male mating success (Surbeck et al. 2019), suggesting that adult males do not directly benefit from maternal social position. However, during immaturity, some offspring may reap the benefits of their mother's social position, as a previous study found that relative maternal rank predicted winning aggressive interactions between individuals < 12 years of age (Markham et al. 2015). The results of these early aggressive interactions may be particularly important for future dominance relationships among males who, as adults, compete for positions in a linear dominance hierarchy that can afford access to fertile females (Wroblewski et al. 2009).

Beyond dominance effects, in many group-living mammalian species, social bonds are associated with increased survival and reproduction (e.g., baboons: Silk et al. 2003, 2009, 2010;

Silk 2007; Archie et al. 2014; Assamese macaques [*Macaca assamensis*]: Schülke et al. 2010; bottlenose dolphins [*Tursiops* sp.]: Frère et al. 2010; horses [*Equus caballus*]: Cameron et al. 2009; humans: Berkman et al. 2004; Holt-Lunstad et al. 2010) and early social experiences can have future fitness consequences (e.g., horses: Nunez et al. 2015; bottlenose dolphins: Stanton and Mann 2012). Recent work in female baboons demonstrated that cumulative early-life adversity, of which maternal loss was one potential source, was associated with both shorter lifespans and lower female-female social connectedness during adulthood (Tung et al. 2016). The mother-offspring relationship provides young mammals with a stable social bond, the loss of which may be a source of psychosocial stress. Both Pusey (1983) and Goodall (1986) described weaned chimpanzees seeking maternal support or reassurance during or following agonistic interactions. The lack of this bond and resulting social support may explain in part the anxiety and depressive behaviors often observed in orphans (Harlow et al. 1965; Suomi 1997; Goodall 1986; Botero et al. 2013) and observed physiological responses, such as increased glucocorticoid concentrations in female baboons following the loss of a close relative to predation (Engh et al. 2006).

While orphaned chimpanzees (aside from older immature females) face increased mortality risk, there is considerable variability in the lifespan of some orphans (Fig. 2). As data on orphan outcomes accumulate, future studies will be necessary to uncover the sources of this variation that are beyond the scope of this study. Maternal dominance rank is one likely candidate as offspring of higher-ranking mothers are more likely to survive (Pusey et al. 1997) and mature faster (Pusey et al. 1997; Walker et al. 2018) than offspring of lower-ranking mothers. Adoption by older community

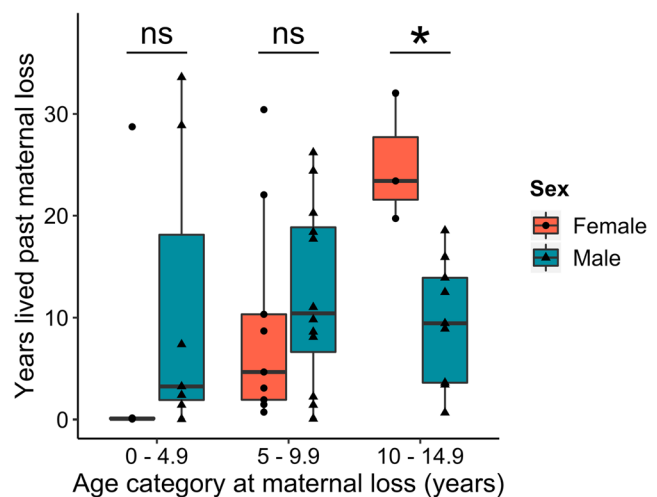


Fig. 2 Sex differences in lifespan following maternal loss for orphans with known death dates in the inclusive sample. Boxplots show median, interquartile range, and 95% confidence intervals. Each point represents the number of years an individual lived post-maternal loss ($N_{\text{male}} = 28$; $N_{\text{female}} = 17$). Permutation tests with Bonferroni correction: $*p < 0.05$; $^{\text{ns}}p > 0.05$

members, most often maternal siblings (Hobaiter et al. 2014), may also contribute to more favorable orphan outcomes. Adoption of orphans has been reported in several chimpanzee populations and studies describe the adopter carrying, defending, sharing food with, and even attempting to nurse the orphan (e.g., Kasekela: Goodall 1986; Wroblewski 2008; Mahale: Nishida et al. 2003; Tai: Boesch et al. 2010; Sonso: Hobaiter et al. 2014; Ngogo: Reddy and Mitani 2019). Presence of an older maternal sibling is associated with higher offspring survival in Gombe's Kasekela community (Stanton et al. 2017) and these kin may be particularly beneficial following maternal loss. Notably, there is currently a lack of consensus regarding the definition of an adoption (see Hobaiter et al. 2014), particularly concerning older orphans who no longer need to be carried. The causes and consequences of adoption is currently an active area of study at Gombe that will allow for a more detailed examination of variation in orphan survivorship in the future.

Overall, our results highlight the importance of maternal care and/or the mother-offspring relationship beyond nutritional dependence and up to adulthood in male chimpanzees, and provide novel evidence for a shorter window of maternal influence on survival for daughters compared to sons. The inclusive fitness benefits of extended maternal care for either offspring or grandoffspring are often cited as adaptive explanations for prolonged post-reproductive lifespans (reviewed in Croft et al. 2015). Notably, while post-reproductive individuals can be found in wild chimpanzee populations, current data suggest this does not represent a distinct life history stage in this species (Emery Thompson et al. 2007; Alberts et al. 2013). As more long-term chimpanzee field sites build datasets integrating demographic, developmental, genetic, health, and physiological data, researchers will begin to be able to uncover the mechanisms through which mothers continue to influence their independent offspring, as well as quantify the potential costs and benefits to mothers themselves of extended maternal association and care.

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Data availability The data analyzed during the current study are available in supplementary material: Online Resource 2.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable international, national, and institutional guidelines for the use of animals were followed. Permission to conduct data collection at Gombe National Park was granted and approved by all applicable governing bodies in Tanzania, including Tanzania National Parks, the Tanzanian Wildlife Research Institute, and the Tanzanian Commission for Science and Technology.

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