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Author(s)	Nakamura, Michio; Hayaki, Hitoshige; Hosaka, Kazuhiko; Itoh, Noriko; Zamma, Koichiro
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Title: Orphaned male chimpanzees die young even after weaning

Authors: Michio Nakamura¹, Hitoshige Hayaki², Kazuhiko Hosaka³, Noriko Itoh¹, Koichiro Zamma¹

Affiliations: ¹Kyoto University, Kyoto, Japan; ²Kobe Gakuin University, Kobe, Japan;
³Kamakura Women's University, Kamakura, Japan

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Key words: *Pan troglodytes*; Mahale; parental care; offspring survival; male-philopatric society

Correspondence to: Michio Nakamura, Wildlife Research Center, Kyoto University, 2-24, Tanaka-Sekiden-Cho, Sakyo, Kyoto, 606-8203, JAPAN.

Phone: +81-75-771-4387 Fax: +81-75-771-4394

E-mail: nakamura@wrc.kyoto-u.ac.jp

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ABSTRACT

If a social-living animal has a long life span, permitting different generations to co-exist within a social group, as is the case in many primate species, it can be beneficial for a parent to continue to support its weaned offspring to increase the latter's survival and/or reproductive success. Chimpanzees have an even longer period of dependence on their mother's milk than do humans, and consequently, offspring younger than 4.5–5 years old cannot survive if the mother dies. Most direct maternal investments, such as maternal transportation of infants and sharing of night shelters (beds or nests), end with nutritional weaning. Thus, it had been assumed that a mother's death is no longer critical to the survival of weaned offspring, in contrast to the case for human children, who continue to depend on parental care long after weaning. However, in theory at least, maternal investment in a chimpanzee son after weaning could be beneficial because in chimpanzees' male-philopatric society, mother and son co-exist for a long time after the offspring's weaning. Using long-term demographic data for a wild chimpanzee population in the Mahale Mountains, Tanzania, we show the first empirical evidence that orphaned chimpanzee sons die younger than expected even if they lose their mothers *after* weaning. This suggests that long-lasting, but indirect, maternal investment in sons continues several years after weaning and is vital to the survival of the sons. The maternal influence on males in the male-philopatric societies of Hominids may be greater than previously believed.

Parental investment (Trivers, 1972) by animals includes metabolic investment in the primary sex cells, nursing, food sharing, protection against predators or group mates, and in the extreme, education in humans. Primate infants, including humans, born in a relatively helpless, altricial state (Nicolson, 1987), depend on their mothers not only for nutrition but also for transportation, protection, thermoregulation, and hygiene. Although such maternal investment decreases with the growth of the offspring, it continues for long periods, up to several years, in some species.

Chimpanzees (*Pan troglodytes*), the closest living species to humans, are no exception. Because a chimpanzee infant depends on the mother's milk for even longer than humans do, it is costly for offspring if the mother dies before weaning. Indeed, it has been reported that wild chimpanzee infants cannot survive when they lose their mothers before they are 4.5–5 years old (Teleki et al., 1976; Goodall, 1983).

Usually, such intense and direct care by the mother ends with the offspring's weaning, especially when the mother resumes estrous and gives birth to the next baby. Almost simultaneously with nutritional weaning, chimpanzee offspring cease to sleep at night with the mother in her bed or nest, are no longer carried by their mothers when travelling, and find and eat food on their own.

Such correspondence of behavioral independence and the end of the requirement for maternal milk in non-human primates may suggest that only humans have a 'childhood' or a period of post-weaning dependence before adulthood (Bogin, 2009). Consequently, it is often assumed that a weaned chimpanzee, unlike a human, can survive even if it loses its mother (Gibbons, 2008). In fact, most weaned chimpanzees did not die with maternal deaths and showed few obvious changes in their health (Goodall, 1986).

Chimpanzees form a male-philopatric unit-group (or community) in which males stay in the natal group and females transfer between groups on maturity (Nishida and Kawanaka, 1972). After an immigrated female gives birth in the new group, she usually stays

in the group until death. This means that a son and his mother typically co-exist in the same group until either of them dies, up to a few decades.

In theory, if a mother and her offspring are in the same social group, it may be beneficial for the mother to support her weaned offspring to increase the latter's fitness, despite some costs. For example, in female-philopatric primate societies, such as those of macaques (*Macaca* spp.), mothers often support their mature daughters to maintain a high dominance rank (Silk, 2009), and because high dominance rank in females is often related with high fertility (Harcourt, 1987), it can be said that maternal support favors the subsequent reproductive success of the daughter. Similarly, in the male-philopatric society of bonobos (*Pan paniscus*), mother-son relationships last even after maturation of the son, and the presence of the mother strongly affects dominance relationships among adult males (Furuichi, 1989; Ihobe, 1992). It has also been reported that the presence of bonobo mothers increased the mating success of adult sons (Surbeck et al., 2011). Recent studies (Foster et al., 2012; Andres et al. 2013) show that in some non-primate mammals, namely killer whales (*Orcinus orca*) and red deer (*Cervus elaphus*), offspring had reduced survival when they lost their mothers after weaning, suggesting that maternal support is crucial for offspring survival.

In chimpanzees, maternal support for a mature son is less obvious, and only a few anecdotal cases have been reported to date. At Gombe and Tai, one mother each supported her son in the competition for raising rank, and the sons eventually acquired alpha status (Goodall, 1986; Boesch, 2009). Some benefits of living mothers can also be inferred from stress-related behaviors of orphans; a recent report showed that orphaned chimpanzees at Gombe increased anxiety-related behaviors and played less frequently (Botero et al., 2013). However, little research has investigated quantitatively the long-term effects of the presence of mothers on the survival of the offspring in wild chimpanzees. We hypothesize that losing a mother, even after weaning, has significant effects on survival of offspring in the longer term, although it may not immediately cause the deaths of orphans. The effects would be expected to be more

apparent in male than female offspring in the male-philopatric society of chimpanzees. Thus, we expect sons who are orphaned after weaning to show a lower survival rate until some age when the mother's presence is no longer vital.

METHODS

We analyzed demographic data for the M group of chimpanzees (Nishida et al., 2003 and unpublished data from the Mahale Mountains Chimpanzee Research Project) inhabiting Mahale Mountains National Park, Tanzania (see Nishida, 2012; Nakamura and Nishida, 2012 for more detail of the study site). The M group has been studied since 1968, but complete identification of central individuals was achieved only in 1980 (Hiraiwa-Hasegawa et al., 1984). However, because some individuals and most of the males had been identified in earlier research, data from 1972 to 2012 were used for analyses.

We observed 37 male orphans whose mothers died before their offspring reached 16 years old (i.e., before adulthood) (Table 1). Most of the orphans' mothers and the orphan's ages were known, but when an unknown young chimpanzee was identified with no mother, we assumed that the individual had been orphaned at the age estimated when first observed. For example, a male, Charles, was first identified in 1993 at an estimated age of 8 years old, not accompanied by his mother. It is very unlikely that an 8 year-old chimpanzee male immigrated to the M group by himself. Thus, we assumed that he was a son of a peripheral female who was seldom observed by the researchers, and soon after he lost his mother, he appeared in the central area. Thus, in this case, we assumed that Charles was orphaned at 8 years old.

In order to examine the consequences of a mother's death on survival of male offspring, we fitted a Cox proportional hazard model (Fox, 2002):

$$h(t) = h_0(t) \exp\{\beta_1 x_1(t) + \beta_2 x_2(t) + \beta_3 x_3(t)\},$$

where

$h(t)$ = hazard rate at time t (years);

$h_0(t)$ = baseline hazard;

$x_1(t) = 1$ if the mother is dead at time t and $t_{\text{or}} < 5$, otherwise 0, t_{or} denotes offspring's age in years when orphaned;

$x_2(t) = 1$ if the mother is dead at time t and $5 \leq t_{\text{or}} < 13$, otherwise 0;

$x_3(t) = 1$ if the mother is dead at time t and $13 \leq t_{\text{or}} < 16$, otherwise 0.

In addition to 37 orphan males, the survival/death data of 63 non-orphan males were also used in this analysis.

Direct comparisons between the sexes are not possible because Mahale females emigrate to neighboring groups at about 9 years old, at the earliest, and we do not have subsequent data on the survival/death of those who were assumed to have emigrated into groups that are not habituated to humans. Therefore, we investigated instead whether female orphans died before or lived up to 9 years old. A total of 19 females were orphaned before 9 years of age.

RESULTS

Table 1 shows the observed survival/death of male chimpanzees who were orphaned before they became full adults (16 years old) in the Mahale M group. Among 37 orphaned males observed so far, only seven lived longer than the expected ages of death. On the other hand, 27 males died before the expected age of death. This difference between observed and expected ages of deaths was statistically significant (Wilcoxon matched-pairs signed-rank test, $T = 521$, $P = 0.00014$). The significance still held when we excluded eight males who were less than 5 years old (*i.e.*, before weaning) at the time they lost their mothers and were thus

more susceptible to their mothers' deaths ($T = 285$, $P = 0.0056$).

Figure 1 shows the probability of survival derived from a Cox proportional hazard model. Males who lost their mothers before their 5th birthday ($t_{\text{or}} < 5$) had a 4.07-fold increase in mortality risk ($P = 0.00038$), and those orphaned between 5 and 13 years ($5 \leq t_{\text{or}} < 13$) had a 2.38-fold increase ($P = 0.013$). However, those orphaned after their 13th birthday ($13 \leq t_{\text{or}} < 16$) did not have a significantly increased mortality risk (hazard ratio = 1.15, $P = 0.84$).

Figure 2 shows the survival/death for male and female orphans. Although all eight of the infant males that were orphaned prior to weaning died almost immediately upon their mothers' deaths, only about half of infant females died after their mothers' deaths (five lived, six died); this difference between the sexes was significant (Fisher's exact test, $P = 0.044$). Furthermore, female orphans had a higher survival rate generally: 10 of 14 females who were orphaned after their third birthdays survived up to the age of possible emigration (9 years old). This ratio did not differ from that of females with live mothers, where 39 of 56 survived (Fisher's exact test, $P = 1.0$).

DISCUSSION

Our results suggest that, in the male-philopatric societies of chimpanzees, the existence of living mothers is important for the survival of sons who stay in their natal group. In particular, it should be noted that the loss of a mother decreased the likelihood of survival not only in infants but also in juveniles and early adolescents in the longer term. These juvenile and adolescent males no longer depended on their mothers' milk and had ceased to receive other direct maternal care, such as bed-sharing or transportation. This indicates that males as juveniles and adolescents receive other types of, presumably indirect and relatively infrequent, benefits from living mothers. Similar to the study of red deer (Andres et al., 2013), a mother's presence affects offspring survival even after weaning.

Male chimpanzees do not become full adults until they are 16 years old (Goodall, 1983; Hiraiwa-Hasegawa et al., 1984), and they often follow the mother for several years after weaning (Pusey, 1983; Hayaki, 1988). By doing so, they may be able to gain benefits by feeding in the same food patch with the mother, sometimes getting shares of meat from the mother, and being groomed more by the mother than *vice versa* (Nishida, 1988). Staying with mothers is also beneficial to the non-adult offspring because they are less likely to be subject to aggression from others than when they are alone (Hiraiwa-Hasegawa and Hasegawa, 1988). There may also be a psychological benefit to being with mothers; it has been reported that some orphaned chimpanzees suffered from a feeling of loss (Goodall, 1983), and following adult males from earlier ages may also cause psychological stress in young chimpanzees. Although male offspring gradually decrease their association with mothers in their juvenile and early adolescent years (Pusey, 1983; Hayaki, 1988), mother-son bonds do not vanish completely. An independent son, when met by his mother, often grooms with her for a long period (Hayaki, 1988). Although not frequent, a mother may also help an adult son at the time of social conflicts with others, and an injured son may stay with his mother until he recovers (Pusey, 1983). Furthermore, some mature males are known to associate frequently with their mothers (Hayaki, 1988). Such possible help of mothers to adult sons may have some similarity with killer whales, whose mothers maintain strong social relations with their adult sons (Foster et al., 2012). However, there is an apparent difference: orphaning did not affect the survival of older chimpanzee sons (13 years or older), whereas killer whale sons faced even higher risk of mortality than did younger sons when they lost their mother (*ibid.*). This may be due to different female reproductive strategies in these two species. Killer whale females have the longest postreproductive life span of all nonhuman animals and continue to support their mature sons throughout their lives. On the other hand, chimpanzee females continue to give birth to new offspring until later in their life span (Emery Thompson et al., 2007). Thus, more investigation is needed on the cost of reduced support to mature offspring

due to care of unweaned younger offspring.

The benefits from mothers or the cost to weaned chimpanzee males of being orphaned may not be readily observable because young males gradually separate from their mothers through their juvenile years and into adolescence, at least superficially (Hayaki, 1988). However, despite the declining frequency of interactions between mother and son, mothers' help to sons may sometimes be critical even after weaning, which may, in the long-term, affect the survival of even young male chimpanzees, as shown in this study. We could not incorporate individual characteristics of orphans' mothers into our analyses, because such data are only partially available in our data set. However, it is possible that such parameters as mother's dominance rank, her past reproductive profiles *e.g.* whether or not she had successfully raised her older children, maternal health before the death, cause of the death, etc. may also have significant effect on the survivorship of the orphan.

Among male-philopatric Hominid species, *i.e.* the *Pan-Homo* clade, maternal support of sons is well known in bonobos. Our study suggests that maternal support of sons also exists in chimpanzees, although the extent may be different. In humans, maternal support of mature daughters, rather than sons, has been emphasized in the context of the 'grandmother hypothesis' (Hawkes et al. 1998). It may be necessary to also consider the possible maternal contribution to mature sons in the course of human evolution.

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Table 1. List of chimpanzee male orphans at Mahale

Name	Mother ¹	Year of birth ²	Age when orphaned (t_{or})(years)	Lived until ³ (years)	Lived longer than expected ⁴
Vandal	Viola	1985	0.6	0.6	No
SO88	Wasobongo	1988	0.9	0.9	No
Tony	Tomato	1986	1.1	1.1	No
FJ06	Fuji	2006	1.2	1.2	No
OP04	Opal	2004	1.7	1.7	No
RB07	Ruby	2007	2.0	2.0	No
Brahim	Betty	1991	2.4	2.4	No
Brutus	Wakampompo	1992	3.5	3.5	No
Chopin	Chausiku	1985	5.4	8.7	No
Darwin	Dar	1988	5.8	23.7+	Yes
Aji	<i>unknown</i>	1973?	6.0	23.0	Yes
Nick	Ndilo	1982	6.6	13.1	No
Kenji	<i>unknown</i>	1970?	7.0	12.0	No
Hiro	<i>unknown</i>	1976?	7.0	15.0	No
Mumu	Momo	1979?	7.0	8.0	No
Oscar	Opal	1998	7.9	7.9	No
Lukaja	<i>unknown</i>	1965?	8.0	26.0	Yes
Charles	<i>unknown</i>	1985?	8.0	14.0	No
Mtwale	Mtimpu	1975?	8.0	14.0	No
Michio	Miya	1996	9.8	16.0+	Undetermined
Kalunde	<i>unknown</i>	1963?	10.0	49.0+	Yes
Fancy	Fanta	1978?	10.0	13.0	No
Hit	<i>unknown</i>	1972?	11.0	16.0	No
Hawazi	<i>unknown</i>	1960?	12.0	15.0	No
Nishida	<i>unknown</i>	1960?	12.0	18.0	No
Kimaro	Adija	1971?	12.0	14.0	No
Sinsi	Fahari	1984?	12.0	13.0	No
Hanby	Happy	1980?	12.0	22.0	No
Toshibo	Wasobongo	1976	12.6	19.2	No
Masudi	Wantendele	1977	12.9	28.7	Yes
Nsaba	Sada	1973	12.9	23.2	No
Bonobo	Wakampompo	1981	14.1	30.7+	Yes
Orion	Opal	1991	15.0	21.1+	Undetermined
Musa	<i>unknown</i>	1957?	15.0	36.0	Yes
Dogura	Dodoma	1981?	15.0	23.0	No
Jilba	Tango	1975?	15.0	21.0	No
Primus	Pinky	1991	15.1	21.2+	Undetermined

¹ When mother was *unknown*, the male was assumed to be orphaned at the time of his first observation with estimated age.

² '?' denotes estimated year of birth.

³ '+' indicates that the individual was still alive at the time of analysis (July 2012).

⁴ The expected age of death at each age (current age + average life expectancy at that age) was calculated from accumulated known age of death of M group males ($n = 96$). 'Undetermined' denotes the male had not reached the expected age of death and was still alive at the time of analysis.

FIGURE LEGENDS

Fig. 1. Survival curves derived from a Cox proportional hazards model for male chimpanzees orphaned at different ages (t_{or}).

Fig. 2. Age classes of orphaned males and females when they lost their mothers and the consequences

Infant: 0 to <5 years old, from birth to weaning. Juvenile: 5 to <9 years old, from weaning to sexual maturity. Early adol.: 9 to <13 years old. Late adol.: 13 to <16 years old.

Although expected ages of death at different ages were calculated for males, those of females could not be calculated because females begin to emigrate at 9 years old (in adolescence); thus survival/death is shown for females up to 9 years old only.

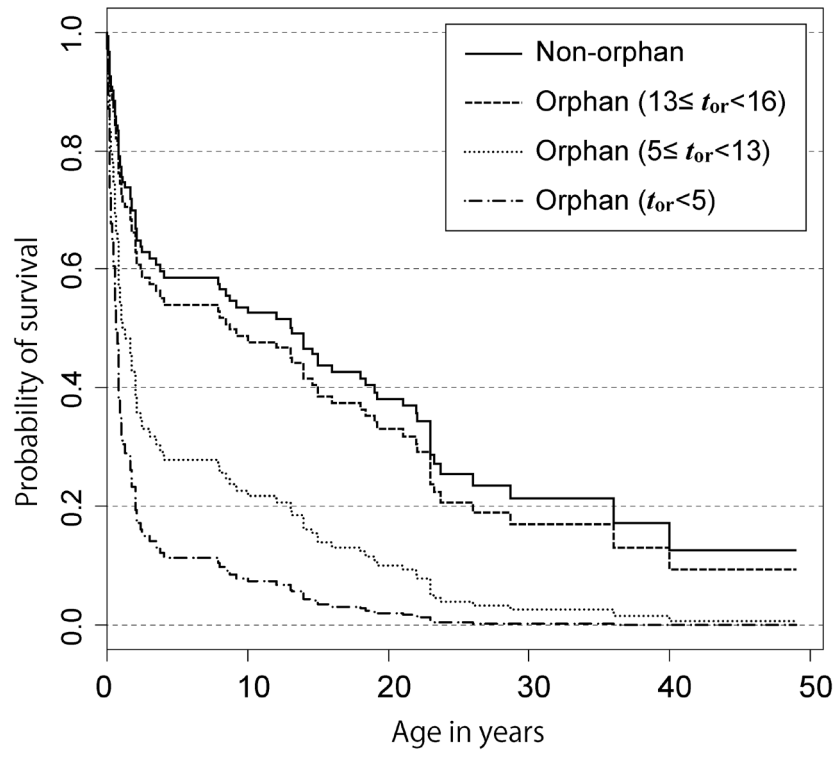


Figure 1

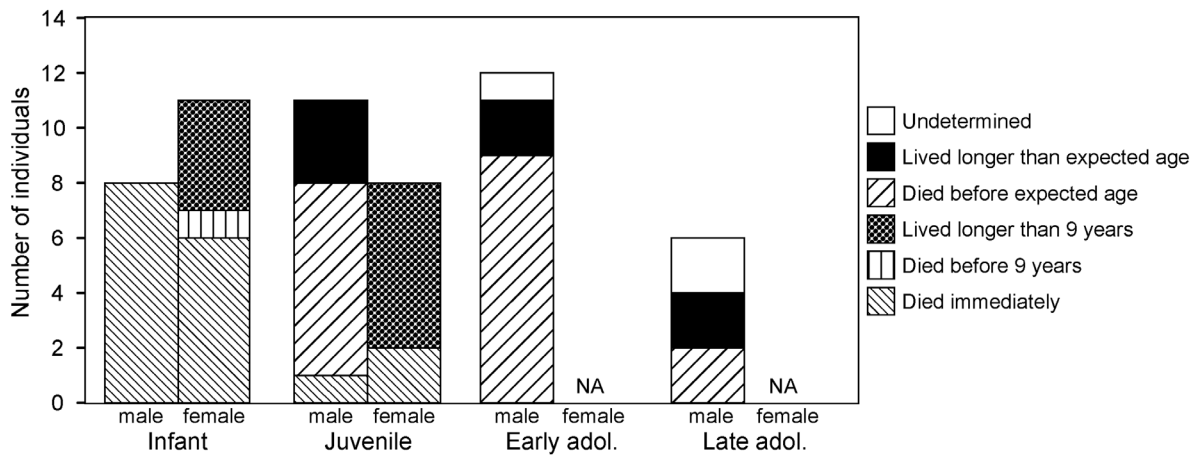


Figure 2