



Do juveniles help or hinder? Influence of juvenile offspring on maternal behavior and reproductive outcomes in wild chimpanzees (*Pan troglodytes*)



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ABSTRACT

Compared to great apes, humans maintain a relatively rapid reproductive pace despite long periods of dependency. This seemingly contradictory set of traits is made possible by weaning offspring before nutritional independence and alloparents who help provide care. In traditional societies, this help may be provided to mothers in part by their juvenile offspring who carry, supervise, or provision younger siblings. In contrast to humans, chimpanzees (*Pan troglodytes*) are nutritionally independent after weaning, yet juveniles continue to travel with their mother and younger sibling for an additional 4–5 years. This continued association could be costly to the mother if she continues to invest in weaned offspring. Alternately, while juvenile chimpanzees do not typically provision younger siblings, their presence and social interaction with infants may allow mothers to focus on other tasks. In this study, we investigate the costs and benefits to mothers of continued association with juveniles in wild chimpanzees. Using 26 years of long-term behavioral data we examined how maternal activity budgets varied based on the presence of a dependent juvenile offspring. We found that continued social interaction between mothers and juveniles does not influence the mother's time allocated to interacting with the younger infant, her feeding, resting, or travel time, or time socializing with other community members. Instead, mothers may benefit from the additional social interaction and/or relationship with their older offspring. Using 45 years of demographic data we found that those offspring who had an older sibling tended to be more likely to survive each year from birth to 8 years than those without an older sibling. Additionally, interbirth intervals were more likely to end when the female had an older offspring present. A mutually beneficial mother-juvenile dynamic in great apes provides insight into continued association between mothers and offspring after nutritional independence and the emergence of juvenile helping during hominin evolution.

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1. Introduction

Compared to other mammals of similar body size, primates are characterized by long, slow periods of growth, delayed sexual maturation, and long lifespans (Harvey et al., 1987; Charnov and Berrigan, 1993). The extended juvenile period between weaning and sexual maturation and the associated delay in reproduction,

which is most pronounced in the great apes and markedly prolonged in humans, is of particular interest. Unlike humans who are weaned relatively early and require additional provisioning (Robson et al., 2006; Bogin, 2009), nonhuman primates are nutritionally independent after weaning. However, despite this nutritional independence, juvenile nonhuman primates of both sexes remain in their natal group where they are thought to benefit from familiar ecological and social environments (Fairbanks, 2000), including continued association with and support from their mothers (Pereira and Altmann, 1985; Fairbanks, 1988; Van Noordwijk, 2012). The majority of existing research on the juvenile period in primates focuses on the adaptive value of this

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developmental stage from the juvenile's perspective, highlighting the benefits of slow and steady growth (e.g., Janson and van Schaik, 1993; Pagel and Harvey, 2002) and time to develop ecological and social competence (e.g., Ross and Jones, 1999; Pereira and Fairbanks, 2002; Cords et al., 2010). Less is known, however, about the costs and benefits to nonhuman primate mothers of continued association and interaction with juvenile offspring. In traditional human societies, mothers typically raise multiple offspring of different ages at a given time. Juvenile humans (~4–10 years of age) can provide benefits to their mothers by contributing to the care of younger siblings through behaviors including carrying, supervising, and provisioning food (e.g., Kramer, 2005, 2011; Konnor, 2010; Crittenden et al., 2013), which, studies suggest, can translate into higher survival of younger siblings (e.g., Sear and Mace, 2008; Nitsch et al., 2013). In this study, we investigate potential costs and benefits of post-weaning maternal care among wild chimpanzees (*Pan troglodytes*).

Compared to chimpanzees, modern humans have lower mortality rates, later maturation, and longer lifespans (Kaplan et al., 2000; Leigh, 2001; Robson et al., 2006; Emery Thompson, 2013). However, despite extensive time and energy investment in offspring, modern human reproductive rates are nearly double that of chimpanzees (Emery Thompson, 2013). Humans maintain the seemingly conflicting combination of large investment with relatively rapid reproduction in part by weaning offspring before they are nutritionally independent (Bogin, 2009). This 'stacking' of dependent offspring is likely a derived feature in *Homo* (Dean, 2006; Robson et al., 2006) associated with the emergence of other distinctive hominin traits, including slow juvenile growth rates (Gurven and Walker, 2006) and reliance on alloparental care (Kramer and Otárola-Castillo, 2015), that allowed for relatively high fertility rates and hominin expansion into novel, ecologically variable environments (Wells and Stock, 2007; Wells, 2012). Recent modeling efforts indicate that early shifts towards modern human life histories could have been supported by help from within mother-offspring groups (Kramer, 2014; Kramer and Otárola-Castillo, 2015). Thus, understanding the trade-offs of post-weaning maternal care in one of human's closest relatives can provide insight into early hominin life history evolution.

According to parental investment theory, maternal resources are finite and investment in one offspring reduces the ability to invest in other offspring (Trivers, 1972). Parental care, however, is a broader term that does not necessarily require such a trade off and encompasses any parental behavior that might increase offspring success (Clutton-Brock, 1991). In addition to costly investment, parental care can also include non-depreciable or 'umbrella' care behaviors such as alarm calling or territorial defense, the benefits of which can be shared across multiple offspring (Lazarus and Inglis, 1986; Clutton-Brock, 1991). The majority of research on post-weaning maternal care in primates comes from female philopatric cercopithecine species (e.g., vervet monkeys [*Chlorocebus aethiops*] and baboons [*Papio* spp.]) that live in stable social groups and exhibit matrilineal rank inheritance (reviewed in Fairbanks, 2000). Thus, it is well established that cercopithecine mothers can play a substantial role in the success of their juvenile and even adult female offspring through access to preferred resources and support in agonistic interactions (e.g., baboons: Cheney, 1977; Lee and Oliver, 1979; Altmann and Alberts, 2005; vervet monkeys: Horrocks and Hunte, 1983).

Unlike the cercopithecines described above, neither chimpanzees nor bonobos (*Pan paniscus*) live in cohesive social groups, but instead exhibit fission-fusion social systems in which party (i.e., subgroup) size and composition are fluid within a larger stable community (Goodall, 1986; Stumpf, 2007). Additionally, in both *Pan*

species males are the philopatric sex, whereas females typically disperse at adolescence (Kano, 1992; Mitani et al., 2002). Despite the lack of a stable social group, evidence for the post-weaning importance of mothers in both *Pan* species is growing. In bonobos, where females can outrank males in the dominance hierarchy (Kano, 1992; Surbeck and Hohmann, 2013), maternal support of sons extends into adulthood as mothers have high rates of association with their adult sons, support adult sons in adult interactions, and maternal presence is associated with increased mating success of sons (Surbeck et al., 2011). In chimpanzees, orphaned males face significantly lower odds of survival than non-orphaned individuals, even if they lose their mothers after weaning. This increased mortality in weaned orphans highlights the importance of some type of post-weaning maternal care in this species (Nakamura et al., 2014). Notably, unlike in bonobos and matrilineal cercopithecine primates, maternal interventions in immature chimpanzee agonistic interactions are rare (Markham et al., 2015), although some maternal interventions in interactions between immatures and adults have been reported (Pusey, 1983; Goodall, 1986). While maternal presence appears to be important to weaned offspring, the rarity of this behavior suggests that maternal interventions are an unlikely source of direct support, at least concerning aggression among peers.

Chimpanzee offspring are nutritionally dependent on their mothers until they are weaned between the ages of 3–5 years (Clark, 1977; Pusey, 1983; van de Rijt-Plooij and Plooij, 1987). While the mother-infant relationship is considered primary, juvenile chimpanzees remain behaviorally dependent and continue to travel with their mothers and younger sibling for 4–5 years after weaning (Pusey, 1983, 1990; Goodall, 1986). Previous investigations suggest that this continued association may come at some cost. For example, Pontzer and Wrangham (2006) found that maternal day range was positively correlated with juvenile body size, but not with infant carrying. Thus, mothers traveling with a behaviorally dependent juvenile, who has not yet reached adult stature, have smaller day ranges than mothers traveling with just an infant, as the juvenile's small size limits how far mothers can range while remaining with their juvenile. Another potential cost to the mother is that of feeding competition with her juvenile offspring, although previous work suggests that competition with juveniles over food resources is unlikely to be a significant cost to mothers, as they were observed to supplant juvenile offspring at feeding sites (Pusey, 1983). Previous studies have also found that mothers remain their juvenile's strongest grooming partner (Pusey, 1983, 1990; Watts and Pusey, 2002), yet whether this attention paid to the juvenile comes at a cost to infant care is unknown. To avoid this trade-off, mothers could either increase their total maternal care budget with two dependent offspring, or the juvenile could offset some of the mother's time investment in the infant. While juveniles in this study community do not habitually carry or provision their infant sibling (Pusey, 1983; Goodall, 1986), they may provide other benefits. These benefits may include a 'safe' social partner such that mothers with juvenile offspring would not need to engage in as much social interaction with their own infants or spend time in parties with other potential social partners, which could allow for mothers to focus on feeding in the absence of other competitors. A recent study among mother-infant pairs in the Ngogo chimpanzee community in Uganda found that increases in infant handling by non-mothers was related to lower lactation effort, which the authors suggest could be indicative of faster weaning and shorter interbirth intervals (IBIs) (Badescu et al., 2016). Early work in Gombe National Park, Tanzania also found descriptive evidence suggesting that mothers with two dependent offspring spend less time with other

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