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Social relationships and caregiving behavior between recently orphaned chimpanzee siblings

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Abstract

When their mothers die, chimpanzees often adopt younger vulnerable siblings who survive with their care. This phenomenon has been widely reported, but few studies provide details regarding how sibling relationships change immediately following the deaths of their mothers. A disease outbreak that killed several females at Ngogo in Kibale National Park, Uganda, furnished an opportunity to document how maternal death influenced the social relationships of siblings. We describe social interactions between four adolescent and young adult males and their younger immature maternal siblings 9 months before and 8 months after their mothers died. We also show how the behavior of individuals in the four recently orphaned sibling pairs contrasts to the behavior displayed by chimpanzees in 30 sibling pairs whose mothers were alive. Following the death of their mothers, siblings increased the amount of time they associated, maintained spatial proximity, groomed, reassured, and consoled each other. During travel, younger orphans followed their older siblings, who frequently looked back and waited for them. Both siblings showed distress when separated, and older siblings demonstrated heightened vigilance in dangerous situations. Chimpanzees who were recently orphaned interacted in the preceding ways considerably more than did siblings whose mothers were alive. These findings suggest that siblings provide each other support after maternal loss. Further research is needed to determine whether this support buffers grief and trauma in the immediate aftermath of maternal loss and whether sibling support decreases the probability that orphans will suffer long-term consequences of losing a mother if they survive.

Keywords

Chimpanzee; Orphans; Kin relationships; Adoption; Altruism; Alloparenting

Introduction

In several species, individuals gain fitness benefits by developing social bonds with conspecifics (Silk et al. 2003, 2009, 2010; Cameron et al. 2009; Schülke et al. 2010). During

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youth, most mammals form strong and dependent relationships with their mothers. Mothers nurse their offspring during infancy and may continue to furnish support, protection, and comfort for many years after weaning them. Consequently, young mammals who lose their mothers often die. Orphans may survive, however, if they find another individual who provides care similar to a mother's. Maternal-like caregiving or "adoption" of such vulnerable orphans has been documented in the wild in many mammals [red squirrels: Gorrell et al. (2010); African wild dogs: McNutt (1996); bottlenose dolphins: Howells et al. (2009); elephants: Goldenberg and Wittemyer (2017); elephant seals: Riedman and Le Boeuf (1982); savanna baboons: DeVore (1963), Altmann (1980), and Hamilton et al. (1982); hamadryas baboons: Kummer (1968); chimpanzees: Goodall (1983, 1986), Boesch et al. (2010), and Hobaiter et al. (2014); bonobos: Surbeck and Hohmann (2017); mantled howler monkeys: Clarke and Glander (1981); red howler monkeys: Agoramoorthy and Rudran (1992) and Struhsaker (2008); ring-tailed lemurs: Gould (2000); black and white colobus monkeys: Dunham and Opere (2016); black-fronted titi monkeys: Cäsar and Young (2008)]. Caregiving by adopters includes nursing and food-provisioning, carrying, active vigilance during group travel, defense, grooming, and comforting behavior. Although individuals of different age and sex classes adopt orphans, older maternal siblings, if present, do so most often [e.g., African elephants: Goldenberg and Wittemyer (2017); baboons: Altmann (1980), Hamilton et al. (1982), and Engh et al. (2009); chimpanzees: Boesch et al. (2010) and Hobaiter et al. (2014); red howler monkeys: Struhsaker (2008); ring-tailed lemurs: Gould (2000); primates generally: Thierry and Anderson (1986)]. This is unsurprising functionally and behaviorally. By helping their kin, older siblings can improve their inclusive fitness (Hamilton 1964), and in species where offspring maintain social relationships with their mothers after weaning, maternal siblings often share strong social bonds [reviewed in Kapsalis (2004)]. Although sibling bonds are already strong, older sisters or brothers who adopt their younger siblings may take on a new parent-like role in the relationship, even if they are still immature [e.g., African elephants: Goldenberg and Wittemyer (2017); baboons: Altmann (1980), Hamilton et al. (1982), and Engh et al. (2009); chimpanzees: Hobaiter et al. (2014)]. As they do so, their pre-existing relationships may intensify and change.

Young chimpanzees who lose their mothers are extremely vulnerable. They navigate a constantly changing social environment and require considerable amounts of care during long periods of dependency (van Lawick-Goodall 1968; Pusey 1983). Chimpanzees are born into social groups of 20–200 individuals, but the first bonds they form are with their mothers and maternal siblings (van Lawick-Goodall 1968; Pusey 1983; Goodall 1986). From birth, chimpanzees are carried, nursed, groomed, and gently touched and comforted by their mothers (van Lawick-Goodall 1968). They receive similar affection from their siblings, who are typically at least 5 years older (Pusey 1983). Mothers stop carrying and nursing their offspring when they are around 5 years old, but for several years thereafter they maintain close spatial proximity and groom with them. Mothers also defend their offspring against aggression and wait for them during group travel. Although chimpanzees constantly fission and fuse to form temporary parties that vary in size and composition (Nishida 1968), young chimpanzees travel almost constantly with their mothers and her other immature offspring (< 12 years) until mid-adolescence (van Lawick-Goodall 1968, Goodall 1986; Pusey 1983,

1990; Hayaki 1988). During late adolescence (ca. 13 years), female chimpanzees disperse to a new community, while males remain in their natal community for life, retaining relationships with their mothers but primarily traveling with other adult males, including their older maternal brothers (Goodall 1986; Hayaki 1988; Pusey 1990). As adults, maternal brothers often maintain strong, long-lasting relationships and cooperate in several different contexts (Langergraber et al. 2007; Mitani 2009).

When chimpanzee mothers die, immature orphans are often adopted by a maternal sibling if they have one (Goodall 1983; Boesch et al. 2010; Hobaiter et al. 2014). The care provided by siblings usually ensures that orphans survive, as long as they are at least 4.5 years old (Hobaiter et al. 2014). Several studies have documented adoption in chimpanzees and noted the remarkable care provided by both maternal relatives and non-relatives. This includes carrying, defense, food sharing, and even nursing (Goodall 1983; Boesch et al. 2010; Hobaiter et al. 2014). These reports, however, provide few detailed observations of how maternal siblings who adopt younger sisters or brothers behaved immediately before and after the deaths of their mothers.

A disease outbreak at Ngogo in Kibale National Park, Uganda (Negrey et al. 2019) furnished an opportunity to investigate the social behavior of orphaned siblings in the aftermath of maternal death. Specifically, we recorded how adolescent (9–15 years) and adult (> 15 years) siblings, who already shared bonds with their younger, immature (< 12 years) siblings (Pusey 1983; Goodall 1986), transitioned to caregiver roles after their mothers died. To further contextualize this transition, we compare the behavior of orphans to the behavior of other siblings whose mothers were alive. We pay special attention to social interactions that may place emotional and cognitive demands on siblings who were caregivers and include several narrative anecdotes to illustrate these and how sibling relationships were influenced by maternal death.

Methods

Study site and subjects

Research took place at Ngogo in Kibale National Park, Uganda, a mid-altitude rainforest (Struhsaker 1997). Members of the Ngogo chimpanzee community occupy a territory of approximately 35 km^2 and have been followed continuously since 1995. The ages of most subadults and young adults in the community are known within 1 month–1 year, while the ages of older individuals are estimated on the basis of their genetic relationships to other individuals, physical appearance, and behavior (Wood et al. 2017). R.R. conducted behavioral observations over 20 months from June to August 2014, June to August 2015, and June 2016 to August 2017, with focal observations of adolescent (9–15 years) and young adult (16–20 years) males initiated in 2015.

During this study, the Ngogo chimpanzee community size ranged between 181 and 219 individuals, fluctuating as a result of immigrations, emigrations, births, and deaths. Twenty-five chimpanzee deaths occurred during a respiratory outbreak that began at the end of December 2016 and lasted through the start of February 2017 (Negrey et al. 2019). During

the epidemic, 13 individuals (age 6–31 years) lost their mothers. Nine of the 13 orphans were under the age of 12, and all but one had at least one surviving maternal sibling.

We studied the behavior of 20 adolescent and 10 young adult male chimpanzees who were part of a study on social development by R.R., and observed for at least 25 h (mean ± SD = 47.8 ± 6.9 h per focal subject). Of these 30 males, 24 had one or two maternal siblings present in the community who were immature and between 4 and 16 years younger than themselves. These younger immature siblings ranged from birth to 10 years old and included 27 individuals, seven of whom were the younger sibling of two focal males. Focal males and their younger, immature maternal siblings formed 34 unique pairs. Four of these pairs were orphaned during the outbreak and serve as case studies in this paper: Nelson (10 years old) and his sister, Amina (6 years old); Damien (11 years old) and his sister, Etta James (6 years old); Yo Yo (11 years old) and his sister Joya (6 years old); and Buckner (17 years old) and his brother Holland (7 years old). We observed these orphaned pairs 9 months prior to and 8 months following their mothers' deaths. The remaining 30 pairs had mothers who were alive throughout the study or for their entire lives. In one case, a focal male, Benny, disappeared and presumably died during the epidemic with his mother. Seven males had infant siblings who were born or died during the study (Table 1). All other sibling pairs were observed during the entire study.

In addition to focal observations, we report ad libitum observations of recent orphans who were focal subjects as well as observations of three additional sibling pairs following the deaths of their mothers: Rosa (11 years old) and her brother, Rich Bergl (4.5 years old), orphaned in 2015; Wayne (21 years old) and his brother, Bach (8 years old) orphaned in January 2017 during the epidemic; Rollins (31 years old) and his sister, Etta James (6 years old) whose brother Damien (11 years old) was R.R.'s focal subject and was also orphaned during the epidemic. In a supplement, we describe the behavior and social relationships of recent orphans who lacked maternal sibling support.

Behavioral observations

R.R. recorded behavioral observations of chimpanzee maternal siblings during focal following episodes of adolescent and young adult males. Observation sessions typically lasted 3 h. After following one focal chimpanzee for 3 h, R.R. switched to a new subject. If no other focal chimpanzee was present, she remained with her current subject for 5 h before leaving to search for a new one. In rare instances where no additional focal individual was available and there were no signs of other chimpanzees, males were followed for more than 5 h.

R.R. recorded chimpanzees in association with her focal subjects every hour. Individuals within visual range of each other were defined to be in association. Chimpanzees in close spatial proximity to focal subjects, i.e., 5 m, were noted every 10 min. Grooming bout durations were recorded to the nearest second, with the individual who initiated a grooming bout noted when possible. We recorded grooming given and received by focal subjects, as well as mutual grooming. We noted all instances of comforting or reassurance behavior, which included affiliative touches such as embracing, hand-holding, mouthing, genital-

rubbing, gentle touching, and mounting that occur frequently between mothers and offspring as well as other chimpanzees who share affiliative bonds (Goodall 1986).

Other behaviors that allowed individuals to maintain close proximity to one another or to maintain association while traveling, including who waited for, approached, left, and followed whom, were noted ad libitum. Specifically, we defined focal subjects as approaching another individual if they came within 5 m of them and no other chimpanzees and stopped. We scored focal subjects as receiving an approach if another individual did the same to him. If focal subjects or other individuals left this 5-m space, focal subjects were designated as leaving or being left by another chimpanzee. If an individual "approached" focal subjects when they were traveling, or vice versa, we recorded our focal subject receiving a "follow" from this individual or that our focal subject "followed" this individual. Sometimes a focal chimpanzee stopped while traveling and looked back, occasionally standing bipedally or actually backtracking to reunite with another individual. When this occurred and the pair continued to travel in the original direction, we noted that the focal subject "waited" for the other chimpanzee. Alternatively, when a chimpanzee behaved this same way toward our focal subject, we scored this individual as having been the recipient of "waiting." "Waiting" was also recorded if a focal chimpanzee finished feeding then sat below the tree where another individual was feeding and remained there until the other individual came down, even if the group traveled on. In this study, we classified these following and waiting behaviors as "travel vigilance." These vigilance and waiting behaviors are typically shown by mothers to their dependent offspring (Pusey 1983) and by adults who have adopted orphans in other populations (e.g., Boesch et al. 2010). We also recorded instances where focal chimpanzees supported or received support from their siblings when they were targets of aggression. Aggression included displays, threats, chases, charges, and attacks involving contact aggression (Goodall 1986). We recorded acts of support when chimpanzees intervened in an ongoing dispute involving their sibling.

Ad libitum observations of social behavior involving nonfocal subjects were also recorded. We report these ad lib observations because they provide information on a larger number of sibling pairs. Because focal and ad libitum data were collected differently, we do not combine them. We use ad libitum data to highlight unusual incidents that provide insights into the cognitive or emotional demands placed on older sibling caregivers.

Data organization and analysis

We investigated how maternal death influenced sibling relationships in three ways. First, we compared the behavior of the four chimpanzee sibling pairs before and after their mothers died. Second, we assessed how the behavior of individuals in the four orphaned pairs differed from the behavior of siblings whose mothers were alive. Third, we investigated the roles each sibling played in their relationship after being orphaned.

We calculated rates of association (percentage of total following episodes in association), proximity (percentage of total proximity scans in proximity), grooming (minutes per hour), reassurance, and travel vigilance between the 24 male subjects and their 27 younger, immature siblings. Calculations for travel vigilance included only younger siblings who moved independently of their mothers (n = 19 maternal siblings, 22 focal subjects, 24 pairs).

For the denominators of the above values, we used the number of following episodes, scan samples, or focal observation hours recorded for a particular focal subject while his sibling was present in the community. For the four orphaned pairs, we calculated two rates for all the preceding measures, one rate for observations made before individuals lost their mothers and another rate after their mothers died. We used a series of generalized linear mixed model (GLMM) analyses to determine how maternal loss influenced the frequency with which (1) a sibling pair associated, (2) maintained spatial proximity, (3) groomed, (4) reassured, and (5) displayed vigilance when traveling. In each analysis, one of the preceding variables was the outcome and the main predictor was whether or not a given sibling pair was orphaned. We included orphaned pairs twice in these analyses, once as orphans, and once as siblings with living mothers. Doing so allowed us to make three behavioral comparisons. We compared orphaned siblings before maternal death to siblings with living mothers, orphaned siblings before maternal death to themselves after maternal death, and orphaned siblings after maternal death to siblings with living mothers. To account for the fact that orphaned individuals and others (Table 1) appeared multiple times in this data set, we included the identities of focal subjects and maternal siblings as random effects. We controlled for observation time by including it as an additional fixed effect. We controlled for age difference between siblings in a similar manner because we expected siblings close in age to interact more often than those separated by many years (cf. Mitani et al. 2002).

We investigated how the dynamics of social relationships between recently orphaned chimpanzees changed after their mothers died. We determined each orphaned sibling's role in the relationship in two ways. We start by reporting how often each sibling initiated grooming and reassurance behavior and how equally grooming was given and received. Next, we determined who was responsible for maintaining spatial proximity. From our "approach" and "leave" data, we created two "proximity maintenance scores" for each of the recently orphaned sibling dyads. One score indicated the focal subject's responsibility for maintaining spatial proximity and the other indicated his sibling's score. Scores were calculated as follows:

Focal subject's proximity maintenance score = number of approaches to sibling − number of leaves from sibling.

Sibling's proximity maintenance score = number of approaches received by focal − number of leaves received by focal.

Positive proximity maintenance scores indicate that an individual approached their sibling more often than they left them. A score of zero indicated that they approached and left them an equal number of times, and a negative score indicated that an individual left their sibling more often than they approached them.

We used ad libitum observations to describe grooming, reassurance, and vigilance behavior involving all recently orphaned siblings shown in Table 1 as well as interactions between orphaned pairs Rosa and Rich Bergl, Wayne and Bach, and Rollins and Etta James. These observations included carrying during travel and defense against aggression from other individuals.

All data were entered into Microsoft Excel and organized and analyzed using the software R and the packages lme4 and lmerTest. Raw data files are included in our supplement. For our GLMM analysis, we employed *z*-score standardization to account for the different scales of the variables. We report effect sizes and standard errors for main effect predictors. We also report *P* values to guide interpretation of results.

Results

Changes in sibling relationships following maternal death

Association and proximity—Recently orphaned siblings altered their behavior in the immediate aftermath of losing their mothers. All orphaned pairs associated while their mothers were alive (mean ± SD = 58% ± 33% of the time), but they did so more often after losing their mothers (mean ± SD = 84% ± 18% of the time). The four orphaned pairs also associated more frequently (mean ± SD = 84% ± 18%) than other siblings whose mothers were alive (mean ± SD = 45% ± 24% of the time; Fig. 1a). A GLMM analysis revealed that, when controlling for age difference, recent orphans associated 6.05 (SE 1.79) times more often than siblings with living mothers (Table 2). This pattern varied with the age of individuals in each pair. In three orphaned pairs both siblings were immature and traveling regularly with their mother before she died. In contrast, Buckner and his younger brother Holland did so less frequently when their mother was alive because Buckner was an adult and already traveling independently (Fig. 1a).

All orphaned pairs maintained proximity to their younger siblings while their mothers were alive, with those close in age doing so most often (mean ± SD = 19% ± 16% of the time; Fig. 1b). After their mothers died, orphans stayed near to each other more than they had previously (mean ± SD = 25% ± 10% of the time) and more so than did other pairs of siblings whose mothers were alive (mean ± SD = 9% ± 9% of the time). A GLMM analysis indicated that males in the four orphaned pairs maintained spatial proximity to their younger, immature siblings 0.42 (SE 0.19) times more often than males with living mothers (Table 2). This shift was less pronounced for orphans who were immature and frequently near each other and their mother when she was alive. After his mother died, 10-year-old Nelson actually spent less time in association with and in proximity to his younger sister, Amina, but Amina was still the individual with whom he maintained proximity most often. All four focal subjects had their younger sibling as their top proximity partner after being orphaned.

Grooming—Chimpanzees in three of the four orphaned sibling pairs groomed each other while their mothers were alive (Fig. 2a). The exception was Buckner and Holland. In contrast, all four pairs groomed after being orphaned, and did so at considerably higher rates (mean ± SD = 3.03 ± 2.15 min/h) than they had when their mothers were alive (mean ± SD = 0.13 ± 0.09 min/h; Fig. 2a). All four orphaned focal males had his younger sibling as his top grooming partner. Grooming occurred between individuals in just 43% (13/30) of the sibling pairs whose mothers were alive. Still, they groomed each other at lower rates than did orphaned siblings (mean ± SD = 0.05 ± 0.09 min/h). A GLMM analysis revealed that, when controlling for age difference, grooming between orphaned siblings occurred 2.07 (SE 0.19) times more often than in dyads whose mothers were alive (Table 2).

Reassurance

Individuals in three of the four orphaned pairs displayed reassurance while their mothers were alive, but they did so rarely, just six times (mean ± SD = 1.5 ± 1.3 times per pair). After losing their mothers, all orphaned siblings reassured each other, and they did so frequently 31 times (means ± SD = 7.8 ± 1.5 times per pair; Fig. 2b). Reassurance between orphans occurred considerably more often than between siblings whose mothers were alive. Individuals in just 33% (10/30) of these pairs displayed reassurance 29 times (means ± SDs = 0.96 ± 1.97 times per pair). Orphaned chimpanzees reassured their younger siblings 1.22 (SE 0.29) times more often than did males with mothers (Table 2, Fig. 2b).

Vigilance

Prior to maternal death, individuals in two orphaned pairs (50%) displayed vigilance while traveling, doing so only one time each (mean ± SD = 0.5 ± 0.58 times per pair). In contrast, individuals in all four orphaned pairs remained vigilant while traveling, doing so 84 times after losing their mothers (mean ± SD = 21 ± 10.1 times per pair; Fig. 2c). Siblings whose mothers were alive looked out for each other while traveling together rarely. They did so only 12 times (mean ± SD = 0.6 ± 0.82 times per pair) in 45% of the pairs (9/20). Orphaned chimpanzee siblings displayed vigilance while traveling 2.64 (SE 0.31) times more often than did siblings whose mothers were alive (Table 2).

Dynamics of sibling relationships following maternal death

We examined how maternal death influenced the dynamics of sibling relationships. Specifically, we investigated who was responsible for initiating grooming, reassurance, and proximity. We recorded 327 grooming bouts between individuals in the four orphaned pairs. Sixty-seven of these bouts had a clear initiator, with younger siblings initiating grooming the majority of the time (64% = 43/67). Grooming, once it began, was not equitable between all dyads, but no clear pattern based on age or age difference emerged.

We recorded reassurance between siblings in the four orphaned pairs 31 times. All but four of these (87%) were initiated by younger chimpanzees and typically involved them approaching and then touching their older sibling with their hand, arm, mouth, or genitals. Two times the older chimpanzee made the initial approach and touched its younger sibling when it screamed or cried. Two other times both siblings approached each other simultaneously. This behavior occurred when both seemed frightened as a result of adult males displaying nearby or because calls of neighboring chimpanzees were heard.

Younger siblings were responsible for maintaining spatial proximity to their older siblings (Fig. 3). Proximity maintenance scores indicated that older siblings were more likely to “leave” their younger sibling than vice versa. These scores do not explain the situation completely because qualitative observations suggest that older siblings were still concerned about the welfare of the younger orphan. Older siblings left their younger siblings, but they often did so at the start of travel. During travel, they were followed by their younger siblings more often than vice versa. While traveling, however, older siblings often waited and looked back for their younger sibling, typically without the latter crying or soliciting the attention of

the former. Thus, by waiting, older siblings appeared to be maintaining associations with and keeping a watchful eye on their orphaned younger siblings.

Ad libitum observations of changes in sibling behavior following maternal death

Ad libitum observations of recently orphaned chimpanzees under age 12 reinforced patterns that emerged from the preceding analyses of focal observation data. Orphaned siblings associated and maintained proximity. Orphaned siblings groomed each other, and younger siblings groomed older siblings more often than the reverse. Similarly, older siblings reassured their younger orphaned siblings, with the latter typically initiating such behavior. Young orphaned chimpanzees followed their older siblings. Finally, older siblings waited for their younger siblings, sometimes stopping and looking back for them while traveling.

Aggression toward immature orphans occurred rarely. We therefore have few observations of older siblings defending younger chimpanzees. Anecdotally, older siblings remained attentive to their younger siblings and helped them when they received aggression from others. On some occasions, older siblings looked toward a scream and approached the source of the call. A few times, they intervened, directing aggression to the chimpanzee who had caused their younger sibling to scream. For example, an adolescent male, Billy Bragg (12 years old), displayed at orphan Holland (7 years old) when Holland attempted to climb and feed in a small *Uvariopsis* tree. Holland's brother, Buckner (17 years old) then leapt to this tree from a nearby one, became piloerect, and charged Billy Bragg, who stopped displaying. Holland was then able to feed. Chimpanzees with mothers also occasionally attended to the screams of their siblings in ways similar to those described here. Still, such behavior, much like that shown during travel, intensified and became more frequent between siblings whose mothers had recently died.

In addition to grooming, reassurance, traveling, and defense, an adolescent female Rosa (11 years) carried her infant brother, Rich Bergl (4.5 years old) dorsally while traveling in the month following their mother's death. Once, this carrying was prompted by Rich Bergl. As he cried, he put his arms around Rosa's back and then jumped on. At first, Rosa pushed him off, but later, as the group traveled quickly Rosa paused and gestured for him to "climb on" (cf. Hobaiter et al. 2014). Rich Bergl continued to ride as Rosa moved a long distance. Other than Rich Bergl, who was the youngest surviving orphan, most orphans were no longer consistently riding on their mother's back when she died. Non-orphans also occasionally carried their maternal siblings and unrelated infants while traveling. Unlike the case above, carrying was not initiated by crying on the part of the younger sibling and did not occur during concerted long-distance group travel. Rather, dorsal and ventral carrying between non-orphans was often initiated by older siblings, who picked up younger ones, sometimes during play, and placed them on their backs or chests, or by the younger sibling playfully hopping onto the older sibling's back (e.g., Goodall 1986).

Some anecdotal observations may reveal emotions that emerge in sibling relationships after maternal death for both older and younger siblings. For example, adolescent chimpanzees occasionally whimper or cry when they fall behind the group or another individual such as their mother. Twice, however, adolescent orphans (Rosa, 11, and Nelson, 10), cried as they searched for their younger siblings. In both cases, the older orphans cried, ran around

frantically among a party of chimpanzees, and stopped crying after finding their siblings. After maternal death, young orphans sought frequent reassurance from their older siblings, but they did so in a qualitatively different way. For example, 7-year-old orphan Holland seemed to seek almost constant physical contact with his 17-year-old brother, Buckner. Holland would regularly sit so that his shoulder touched Buckner's and often, while Buckner sat upright, Holland pressed his own back into Buckner's chest or shoulder, occasionally whimpering (Fig. 4). This continued for at least 8 months after their mother's death.

Additional observations suggest that older siblings showed heightened vigilance in times of danger. Eight months after Kanawa's death in 2017, her offspring Rollins (31 years old), Damien (11 years old), Etta James (6 years old), and an unrelated adolescent male, Billy Bragg (12 years old), traveled into the territory of neighboring chimpanzees. Being in this area, especially in small numbers or alone, is dangerous for chimpanzees (Wilson and Wrangham 2003; Mitani et al. 2010). While there, the chimpanzees in this group were extremely quiet and moved carefully checking trees for fruit. None of the males stopped to feed in any of the trees, but Etta did on two occasions, and both times, Rollins sat below the tree and waited for her to start and finish feeding and come back to the ground before moving on. He also regularly looked back for both of his siblings while they continued to move in the territory of their neighbors. As they returned to the Ngogo territory and met other community members, Rollins moved farther ahead of Damien and Etta and no longer waited below trees where they stopped to feed unless he too, fed there.

Finally, some siblings altered their behavior in similar ways when their mothers were still alive and temporarily absent or on a sexual consortship (Tutin 1979). Consorting behavior by adult female Kanawa, who later died, allowed us to observe some of these dynamics. Prior to her death, Kanawa went on two consortships that lasted up to 2.5 months, one in 2015 and another in 2016. During these episodes Kanawa left both Etta James and Damien behind. The first time Kanawa left, Rollins was 29 years old, Damien was 9 years old, and Etta James was 4 years old. One time Rollins and two other adult males crossed paths with a group of adult females and their offspring and Damien and Etta James. The adults in both parties continued traveling in opposite directions but Damien stopped and turned around to follow Rollins instead of the group of females. Etta, however, had already gone ahead with the adult females and was out of view. As Rollins kept traveling, Damien paused, stood up on two legs, and looked back. He continued to do this, while moving short distances toward his older brother. Finally, Etta appeared alone, whimpering, and Damien, still standing bipedally, looked over to her. She began screaming and ran to him. Damien embraced her and she fell quiet. After this, he let go and began running quickly to catch up to Rollins with Etta following. The siblings remained together until late in the evening. When Kanawa returned, Damien no longer waited or looked back for Etta. Importantly, Damien appeared to keep a watchful eye on Etta in the absence of her seeking his attention.

Discussion

After losing their mothers, recently orphaned chimpanzees intensified their social interactions with at least one of their maternal siblings if they had one. If both orphans were close in age and immature (< 12 years) and had thus almost always been together with their

mother prior to her death, they continued to do so after she died and interacted even more frequently. In addition, mature chimpanzees, who had interacted only occasionally with their younger siblings prior to losing their mother, now had them in almost constant company with younger siblings initiating most of the contact. For all adolescent and young adult male focal subjects, their younger immature orphaned sibling became the individual with whom they most often groomed and spent time in close spatial proximity. Furthermore, the rate at which these orphaned siblings interacted was higher than that of siblings whose mothers were alive.

Social interactions between recently orphaned siblings included behaviors that were common, but less frequent between non-orphaned siblings such as maintaining association and proximity and grooming, but also some behaviors that were infrequent or absent between siblings with living mothers. The behaviors that emerged or became regular occurrences only after maternal loss included comforting reassurance acts such as embraces, hand-holding, and mouthing suggested to be important for the emotional development of orphans (Clay and de Waal 2013), as well as extreme vigilance demonstrated during group travel through following, waiting for, and looking for each other. Older orphans also occasionally carried their younger siblings dorsally during travel and defended them against aggression from other chimpanzees when they screamed. Thus, after losing their mother, older siblings appeared to take on a new type of role in the lives of their younger siblings (cf. Hobaiter et al. 2014).

Virtually all social behavior between orphaned siblings was initiated by younger siblings, indicating the active role they played in the relationships. Younger siblings typically started grooming and groomed their older sibling more than they received grooming from them though this was not the case for all pairs. They were almost always the ones to seek reassurance, approach, and maintain spatial proximity, and follow their older siblings during travel. Still, it seemed important to older siblings that this spatial proximity was maintained, especially during travel. While their younger siblings approached and followed, older siblings often waited for them to catch up and finish feeding. Older siblings also looked for their younger brothers and sisters before traveling, sometimes backtracking or standing bipedally to extend their view. This leaving and waiting pattern mirrors that shown by mothers to their dependent offspring; mothers typically leave their juvenile offspring when they begin to travel, but wait for them to follow (Pusey 1983).

Certain behaviors revealed the potential cognitive and emotional demands of caregiving. Older siblings seemed to offer maternal-like care when mothers were absent. For example, adolescent male Damien took care of his younger sister Etta James when their mother, Kanawa, was on consort, but not after she returned. He then resumed this role after Kanawa died. Serving as a caregiver was flexible, and did not necessarily depend on his sister soliciting care, but instead contingent on maternal presence or absence. This flexible, temporary adoptive behavior when a mother is sick or injured has been described in other chimpanzee groups (Uehara and Nyundo 1983; Pruetz 2011). Sibling caretakers also showed heightened vigilance, looking back for siblings and waiting for them to catch up or finish feeding in potentially dangerous situations, such as travel outside of the territory.

This flexible waiting behavior in chimpanzees is of particular interest, because small-bodied juvenile chimpanzees who are not carried during travel may pose a ranging cost to their adopters. Mothers with dependent juveniles have decreased day ranges than mothers with infants who still cling (Pontzer and Wrangham 2006). Pontzer and Wrangham (2006) suggest that this may occur because when small-bodied juvenile offspring cannot keep up with traveling parties, mothers choose to leave parties rather than “abandon” their offspring. Male chimpanzees who adopt their juvenile siblings may be faced with similar choices. For instance, Rollins “abandoned” his trailing 6-year-old sister in a large party with other group members, but was unwilling to do so while traveling with her outside of the territory when he was the only adult. In other chimpanzee groups, both maternal siblings and maternally unrelated adopters are similarly unwilling to leave lagging adoptees behind; instead, they wait for and carry them (Goodall 1983; Uehara and Nyundo 1983; Boesch et al. 2010; Pruetz 2011; Hobaiter et al. 2014). Waiting for, retrieving, and carrying adoptees before group movement is also common in other species whose infants are typically carried by mothers [e.g., baboons: Hamilton et al. (1982); ring-tailed lemurs: Gould (2000)].

Caring for younger siblings appeared to have emotional importance, and perhaps place a toll on older siblings. Specifically, separation from their younger charges occasionally caused older siblings visible distress. They cried until they found their younger siblings. Importantly, crying when separated from a specific individual, while relatively common for infant and juvenile chimpanzees, was rare in the older adolescents who showed this behavior. It is possible that having a sibling, even one who requires considerable care, might buffer an older sibling’s grief. Grief and depression, for both humans and nonhuman animals, may sometimes be buffered by the strengthening of existing relationships and the formation of new ones (Engh et al. 2005; Stroebe et al. 2005; Dopp and Cain 2012). Here, studies of the physiology of these individuals before and after their mothers died would provide important insights into how sibling adoption might affect older siblings. For example, adoption is likely to stress individuals who take on the burden of caring for others, and this might be revealed by comparing the cortisol levels of individuals who adopt others before and after doing so. Other costs incurred by older siblings, who start to care for their younger siblings, constitute an important issue that will require future study. These costs include less time to allocate to feeding and other social relationships that will impact fitness.

Additional research will also be required to document the long-term benefits that older siblings provide younger orphans. Adoption increases the probability that orphans will survive over the short term in chimpanzees (Goodall 1983; Boesch et al. 2010; Hobaiter et al. 2014). However, in several species, even when orphans survive, they can experience decrements in growth, reproduction, and longevity and suffer negative impacts on health, social status, and emotional development [e.g., Asian elephants: Lahdenperä et al. (2016); baboons: Tung et al. (2016); red deer: Andres et al. (2013), humans: Cerel et al. (2006), chimpanzees: Walker et al. (2018), Nakamura et al. (2014); bonobos: Clay and de Waal (2013)]. How sibling adoption buffers orphans against these deleterious consequences in chimpanzees is currently unknown, but it appears to have long-term benefits in some other species (Engh et al. 2009).

In sum, the observations presented in this paper add to a body of literature on the importance of kin relationships and adoptive behavior in chimpanzees [for review, see Hobaiter et al. (2014)] and other mammals [e.g., elephants: Lee (1987); baboons: Engh et al. (2009)]. They also provide insights into the flexibility of caregiving behaviors by males, who, in many primate species, in addition to chimpanzees and baboons described here, adopt infants (Pope 1998; Struhsaker 2008; Gould 2000). Taken together, these findings contribute to our understanding of the evolution of alloparental behavior, an integral feature and part of our own species' behavior that influences offspring survival (Hrdy 2009).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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References

Agoramoorthy G, Rudran R (1992) Adoption in free-ranging red howler monkeys, Alouatta seniculus, of Venezuela. Primates 33(4):551–555

Altmann J (1980) Baboon mothers and infants. University of Chicago Press, Chicago

Andres D, Clutton-Brock TH, Kruuk LE, Pemberton JM, Stopher KV, Ruckstuhl KE (2013) Sex differences in the consequences of maternal loss in a long-lived mammal, the red deer (Cervus elaphus). Behav Ecol Sociobiol 67(8):1249–1258

Boesch C, Bole C, Eckhardt N, Boesch H (2010) Altruism in forest chimpanzees: the case of adoption. PLoS One 5(1):e8901 [PubMed: 20111704]

Cameron EZ, Setsaas TH, Linklater WL (2009) Social bonds between unrelated females increase reproductive success in feral horses. Proc Natl Acad Sci 106(33):13850–13853 [PubMed: 19667179]

Cäsar C, Young RJ (2008) A case of adoption in a wild group of black-fronted titi monkeys (Callicebus nigrifrons). Primates 49(2):146–148 [PubMed: 17938856]

Cerel J, Fristad MA, Verducci J, Weller RA, Weller EB (2006) Childhood bereavement: psychopathology in the 2 years postparental death. J Am Acad Child Adolesc Psychiatry 45(6):681–690 [PubMed: 16721318]

Clarke MR, Glander KE (1981) Adoption of infant howling monkeys (Alouatta palliata). Am J Primatol 1(4):469–472 [PubMed: 31995912]

Clay Z, de Waal FB (2013) Bonobos respond to distress in others: consolation across the age spectrum. PLoS One 8(1):e55206 [PubMed: 23383110]

DeVore I (1963) Mother-infant relations in free-ranging baboons In: Rheingold HL (ed) Maternal behavior in mammals. Wiley, New York, pp 305–335

Dopp AR, Cain AC (2012) The role of peer relationships in parental bereavement during childhood and adolescence. Death Stud 36(1):41–60 [PubMed: 24567994]

Dunham NT, Opere PO (2016) A unique case of extra-group infant adoption in free-ranging Angola black and white colobus monkeys (Colobus angolensis palliatus). Primates 57(2):187–194 [PubMed: 26872896]

Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL (2005) Behavioural and hormonal responses to predation in female chacma baboons (Papio hamadryas ursinus). Proc R Soc B Biol Sci 273(1587):707–712

Engh AL, Hoffmeier RR, Seyfarth RM, Cheney DL (2009) O brother, where art thou? The varying influence of older siblings in rank acquisition by female baboons. Behav Ecol Sociobiol 64(1):97–104

Goldenberg SZ, Wittemyer G (2017) Orphaned female elephant social bonds reflect lack of access to mature adults. Sci Rep 7(1):14408 [PubMed: 29089603]

Goodall J (1983) Population dynamics during a 15-year period in one community of free-living chimpanzees in the Gombe National Park, Tanzania. Z Tierpsychol 61(1):1–60

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge

Gorrell JC, McAdam AG, Coltman DW, Humphries MM, Boutin S (2010) Adopting kin enhances inclusive fitness in asocial red squirrels. Nat Commun 1:22 [PubMed: 20975694]

Gould L (2000) Adoption of a wild orphaned ring-tailed lemur infant by natal group members: adaptive explanations. Primates 41(4):413–419 [PubMed: 30545205]

Hamilton WD (1964) The genetical evolution of social behaviour II. Journal of Theor Biol 7(1):17–52 [PubMed: 5875340]

Hamilton WJ, Busse C, Smith KS (1982) Adoption of infant orphan chacma baboons. Anim Behav 30(1):29–34

Hayaki H (1988) Association partners of young chimpanzees in the Mahale Mountains National Park, Tanzania. Primates 29(2):147–161

Hobaiter C, Schel AM, Langergraber K, Zuberbühler K (2014) ‘Adoption’ by maternal siblings in wild chimpanzees. PLoS One 9(8):e103777 [PubMed: 25084521]

Howells EM, Reif JS, Bechdel SE, Murdoch ME, Bossart GD, McCulloch SD, Mazzoil MS (2009) A novel case of non-offspring adoption in a free-ranging Atlantic bottlenose dolphin (Tursiops truncatus) inhabiting the Indian River Lagoon, Florida. Aquat Mamm 35(1):43–47

Hrdy SB (2009) Mothers and others. Harvard University Press, Cambridge

Kapsalis E (2004) Matrilineal kinship and primate behavior In: Chapais B, Berman CM (eds) Kinship and behavior in primates. Oxford University Press, Oxford, pp 153–176

Kummer H (1968) Social organization of hamadryas baboons. University of Chicago Press, Chicago

Lahdenperä M, Mar KU, Lummaa V (2016) Nearby grandmother enhances calf survival and reproduction in Asian elephants. Sci Rep 6:27213 [PubMed: 27282468]

Langergraber KE, Mitani JC, Vigilant L (2007) The limited impact of kinship on cooperation in wild chimpanzees. Proc Natl Acad Sci 104(19):7786–7790 [PubMed: 17456600]

Lee PC (1987) Allomothering among African elephants. Anim Behav 35(1):278–291

McNutt JW (1996) Adoption in African wild dogs, Lycaon pictus. J Zool 240(1):163–173

Mitani JC (2009) Male chimpanzees form enduring and equitable social bonds. Anim Behav 77(3):633–640

Mitani JC, Watts DP, Pepper JW, Merriwether DA (2002) Demographic and social constraints on male chimpanzee behaviour. Anim Behav 64(5):727–737

Mitani JC, Watts DP, Amsler SJ (2010) Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. Curr Biol 20(12):R507–R508 [PubMed: 20620900]

Nakamura M, Hayaki H, Hosaka K, Itoh N, Zamma K (2014) Brief Communication: Orphaned male chimpanzees die young even after weaning. Am J Phys Anthropol 153(1):139–143 [PubMed: 24318948]

Negrey JD, Reddy RB, Scully EJ, Phillips-Garcia S, Owens LA, Langergraber KE, Mitani JC, Emery Thompson M, Wrangham RW, Muller MN, Otali E (2019) Simultaneous outbreaks of respiratory disease in wild chimpanzees caused by distinct viruses of human origin. Emerg Microbes Infect 8(1):139–149 [PubMed: 30866768]

Nishida T (1968) The social group of wild chimpanzees in the Mahali Mountains. Primates 9(3):167–224

Pontzer H, Wrangham RW (2006) Ontogeny of ranging in wild chimpanzees. Int J Primatol 27(1):295

Pope TR (1998) Effects of demographic change on group kin structure and gene dynamics of populations of red howling monkeys. J Mammal 79(3):692–712

Pruetz JD (2011) Targeted helping by a wild adolescent male chimpanzee (Pan troglodytes verus): evidence for empathy? J Ethol 29(2):365–368

Pusey AE (1983) Mother–offspring relationships in chimpanzees after weaning. Anim Behav 31(2):363–377

Pusey AE (1990) Behavioural changes at adolescence in chimpanzees. Behaviour 115(3):203–46

Riedman ML, Le Boeuf BJ (1982) Mother-pup separation and adoption in northern elephant seals. Behav Ecol Sociobiol 11(3):203–215

Schülke O, Bhagavatula J, Vigilant L, Ostner J (2010) Social bonds enhance reproductive success in male macaques. Curr Biol 24:2207–2210

Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. Science 302(5648):1231–1234 [PubMed: 14615543]

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2009) The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proc R Soc B Biol Sci 276(1670):3099–3104

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2010) Strong and consistent social bonds enhance the longevity of female baboons. Curr Biol 20(15):1359–1361 [PubMed: 20598541]

Stroebe W, Zech E, Stroebe MS, Abakoumkin G (2005) Does social support help in bereavement? J Soc Clin Psychol 24(7):1030–1050

Struhsaker TT (1997) Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation. University Press of Florida, Gainesville

Struhsaker TT (2008) Demographic variability in monkeys: implications for theory and conservation. Int J Primatol 29(1):19–34

Surbeck M, Hohmann G (2017) Affiliations, aggressions and an adoption: male–male relationships in wild bonobos In: Hare B, Yamamoto S (eds) Bonobos: Unique in mind, brain and behaviour. Oxford University Press, Oxford, pp 35–46

Thierry B, Anderson JR (1986) Adoption in anthropoid primates. Int J Primatol 7(2):191–216

Tung J, Archie EA, Altmann J, Alberts SC (2016) Cumulative early life adversity predicts longevity in wild baboons. Nat Commun 7:11181 [PubMed: 27091302]

Tutin CEG (1979) Mating patterns and reproductive strategies in a community of wild chimpanzees (Pan troglodytes schweinfurthii). Behav Ecol Sociobiol 6(1):29–38

Uehara S, Nyundo R (1983) One observed case of temporary adoption of an infant by unrelated nulliparous females among wild chimpanzees in the Mahale Mountains, Tanzania. Primates 24(4):456–466

van Lawick-Goodall J (1968) The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Anim Behav Monogr 1:161–IN12

Walker KK, Walker CS, Goodall J, Pusey AE (2018) Maturation is prolonged and variable in female chimpanzees. J Hum Evol 114:131–140 [PubMed: 29447755]

Wilson ML, Wrangham RW (2003) Intergroup relations in chimpanzees. Annu Rev Anthropol 32(1):363–392

Wood BM, Watts DP, Mitani JC, Langergraber KE (2017) Favorable ecological circumstances promote life expectancy in chimpanzees similar to that of human hunter-gatherers. J Hum Evol 105:41–56 [PubMed: 28366199]

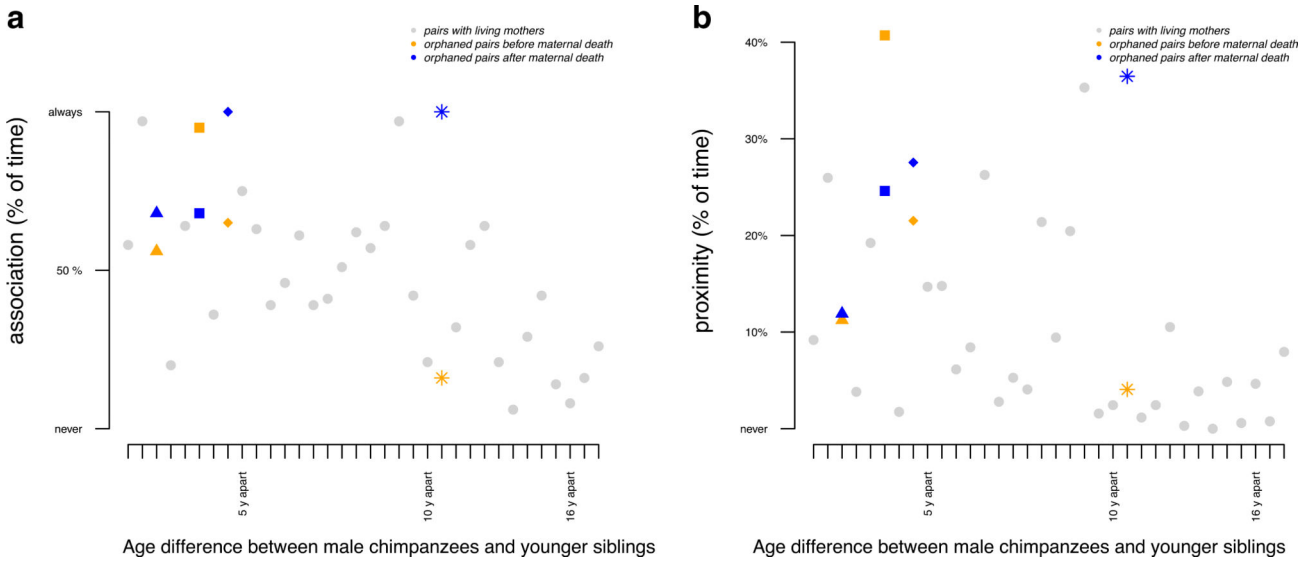

Fig. 1.

Rates of **a** association and **b** proximity between focal males and their younger maternal siblings. Values for orphaned pairs Damien and Etta James (triangles), Nelson and Amina (squares), Yo Yo and Joya (diamonds), and Buckner and Holland (stars) are shown in orange before maternal death (9 months) and in blue after maternal death (8 months). Values for pairs (n = 30) whose mothers were alive (n = 30) are shown as gray circles

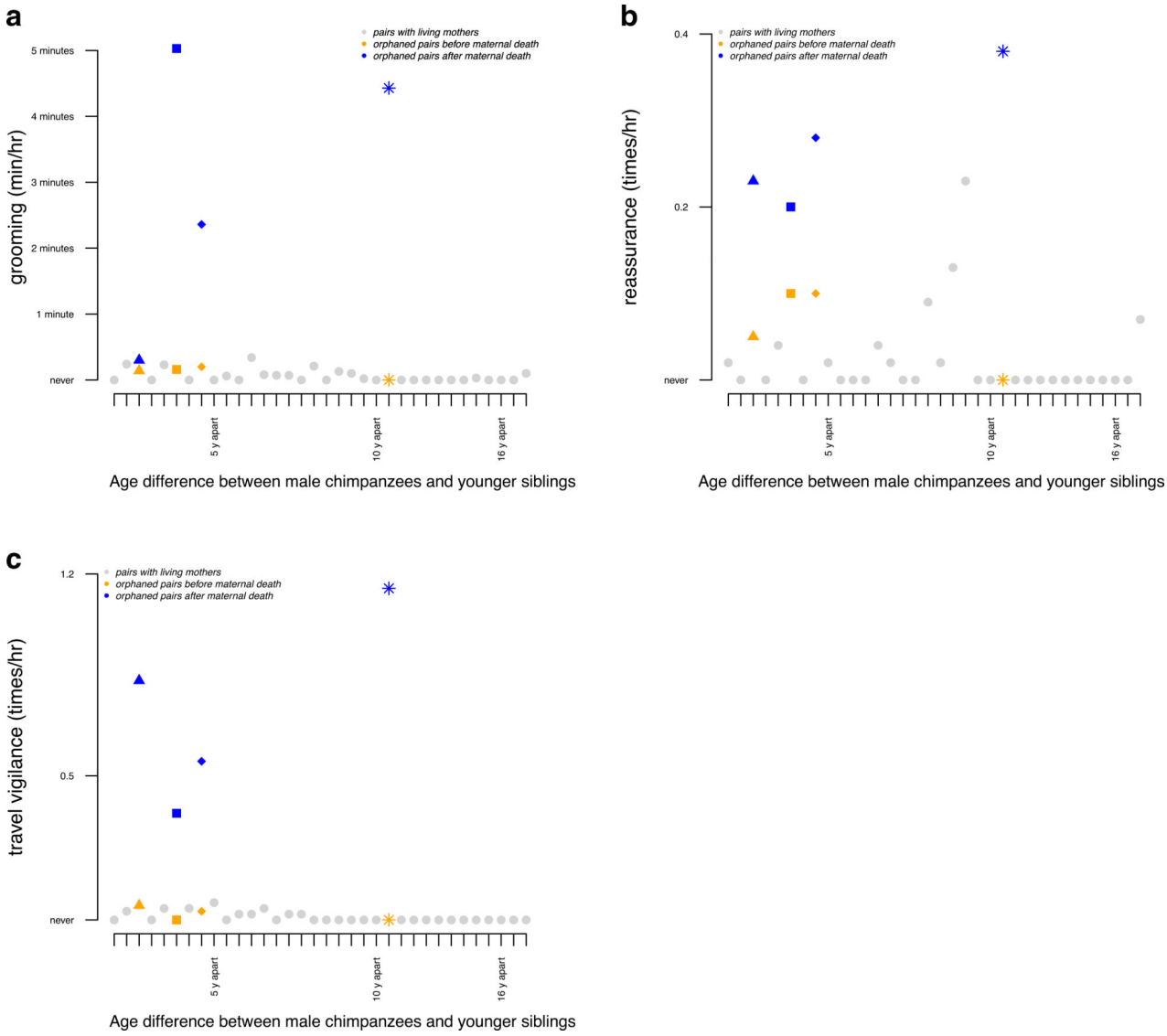

Fig. 2.

Rates of **a** grooming, **b** reassurance, and **c** vigilance while traveling between focal males and their younger maternal siblings. Values for orphaned pairs Damien and Etta James (triangles), Nelson and Amina (squares), Yo Yo and Joya (diamonds), and Buckner and Holland (stars) are shown in orange before maternal death (9 months) and in blue after maternal death (8 months). Values for pairs (n = 30) whose mothers were alive (n = 30) are shown as gray circles

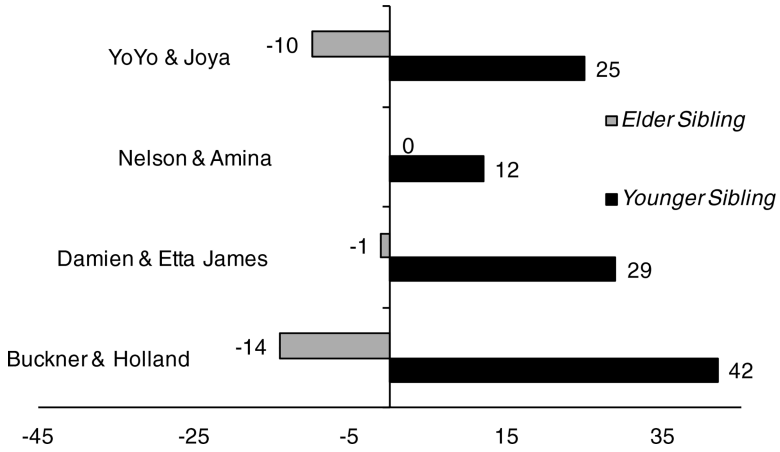

Fig. 3.

Proximity maintenance scores between four orphaned focal subjects and their younger siblings. Positive proximity maintenance scores indicate that an individual initiated and maintained proximity while negative scores indicate that an individual tended to terminate proximity. For each dyad, the proximity score of the older sibling is shown in gray and that of the younger sibling in black. See text for further explanation

Fig. 4.

Young orphan, Holland (right), rests with his arm pressed against his adult brother's (left) shoulder. Recent orphans often sought comfort from older siblings in this manner. Photo by Kevin Lee

Table 1

Focal chimpanzee subjects and their immature maternal siblings

Focal subject	Age	Mother	Younger maternal siblings
Male orphans			
Nelson	10	Anderson (d. 2017)	Amina (f, b. 2010)
Damien	11	Kanawa (d. 2017)	Etta James (f, b. 2011)
Yo Yo	11	Cecilia (d. 2017)	Joya (f, b. 2011)
Buckner	17	Lucia (d. 2017)	Holland (m, b. 2010) Infant (b. 2015, d. 2017)
Males with living mothers			
Cannonball	9	Sigourney	Fricka (f, b. 2011)
Larson	9	Fleming	DiDonato (f, b. 2012) Whitman (m, b. 2016)
Williams	9	Bacall	Elvira (f, b. 2012) Caceres (f, b. 2016)
Gus	10	Sills	Denis (m, b. 2015)
Dylan	10	Fitzgerald	Pilar (f, b. 2013, d. 2017)
Fleck	11	Sarah	Salonen (m, b. 2012)
Billy Bragg	12	Rusalka	Flanagan (m, b. 2011)
Elton	12	Kidman	Cedar (m, b. 2013)
Jarman	12	Callas	Toshi (m, b.2011) Infant (f, b. 2016, d. 2017)
Murray	12	Senta	Struhsaker (m, b. 2011) Junot (m. b. 2016)
Orff	12	Sutherland	Naidu (f, b. 2011)
Bosko	14	Julianne	Josipa (f, b. 2010) Infant (m, b. 2015, d. 2016)
Booker	15	Sills	Gus (m, b. 2007) Denis (m, b. 2015)
Barron	16	Sutherland	Naidu (f, b. 2011)
Chopin	16	Violetta	Bobi Wine (m, b. 2010)
Abrams	17	Callas	Toshi (m, b.2011) Infant (f, b. 2016, d. 2017)
Benny	17	Cecilia	Yo Yo (m. b. 2006) Joya (f, b. 2011)
Lovano	17	Fitzgerald	Dylan (m, b. 2006) Pilar (f, b. 2013, d. 2017)
Wilson	17	Kidman	Cedar (m, b. 2013)
Haden	18	Lita	Muhammad Ali (m, b. 2015)

All subjects are adolescent and young adult male chimpanzees studied between June 2015 and August 2017. Age values indicate ages in January 2017 rounded to the nearest year

Table 2

Results of GLMM analyses where outcome variables are how often siblings in a pair associated, maintained spatial proximity, groomed, reassured each other, and displayed vigilance while traveling. Main effect predictors, their effect sizes, standard errors, and summary statistics are shown. These models assumed a negative binomial distribution and included the identities of focal subjects and their siblings as random effects (n = 24 focal subjects, 27 siblings)

	Estimate	Std. error	*p* value
Association			
Intercept	18.67	1.45	
Age difference	− 7.09	2.26	0.004
Observation time	6.62	2.15	0.005
Orphan status	6.05	1.79	0.004
Proximity			
Intercept	2.89	0.19	
Age difference	− 0.79	0.28	0.005
Observation time	0.46	0.29	0.113
Orphan status	0.42	0.19	0.027
Grooming			
Intercept	0	0.48	
Age difference	− 1.89	0.55	0.001
Observation time	0.78	0.54	0.148
Orphan status	2.07	0.19	< 0.001
Reassurance			
Intercept	− 0.49	0.44	
Age difference	− 0.63	0.74	0.40
Observation time	0.36	0.63	0.57
Orphan status	1.22	0.29	< 0.001
Travel vigilance (n = 24 pairs)			
Intercept	− 0.11	0.27	
Age difference	− 0.28	0.6	0.641
Observation time	0.34	0.55	0.532
Orphan status	2.64	0.31	< 0.001