Dead infant carrying by chimpanzee mothers in the Budongo Forest

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Abstract

It has been suggested that non-human primates (hereafter primates) can respond to deceased conspecifics in ways that suggest they experience psychological states not unlike humans, which would indicate they exhibit some notion of death. Here, we report long-term demographic data from two East African chimpanzee groups. During a combined 40-year observation period we recorded 191 births of which around a third died in infancy, mostly within the first year. We documented the post-mortem behaviour of the mothers and found that Budongo chimpanzee mothers routinely carried deceased infants after their death, usually until the body started to decompose after a few days. However, we also observed three cases of extended carrying lasting for more than 2-weeks, one of which was followed by the unusual extended carrying of a substitute object and another which lasted three months. In each case, the corpses mummified. We discuss these data in view of functional hypotheses of dead infant carrying in primates and regarding the potential proximate mechanisms involved in this behaviour. We suggest that chimpanzees may exhibit psychological processes related to death of conspecifics similar to human grieving.

Introduction

Primate thanatology, the study of the behaviour and underlying physiological and psychological factors associated with dead or dying individuals in non-human primates (hereafter primates), continues to raise important questions about human uniqueness (Anderson 2016, 2018; Anderson et al. 2018). Humans experiencing the loss of socially close individuals experience significant psychological trauma with long-term physiological effects, including symptoms of post-traumatic stress disorder, anxiety and depression, and increased used of health-care resources (Figley et al. 1997; Parkes et al. 1997; Lannen et al. 2008). Given our biological and social similarities, other primate species – in particular other great

apes – may experience similar cognitive and physiological changes. Cross-species comparisons, especially in primates, are often used to reveal past evolutionary trajectories of the hominid lineage. Primate behaviour and physiology in relation to deceased individuals provide valuable data to better understand the origins of why humans are so powerfully affected by death. More generally, primate responses to death may provide further insight into other aspects of animal cognition, such as animacy or the perception of time (Gonçalves and Carvalho 2019).

Because death is unpredictable and rarely observed in wild primate communities, the available datasets are usually anecdotal and descriptions of events are often incomplete (Watson and Matsuzawa 2018; Ramsay and Teichroeb 2019). Nevertheless, an increasing number of primate groups have been habituated to human observers (Kappeler et al. 2012), which has led to more frequent reporting and more systematic efforts to extract patterns of behaviour in responses to death (Anderson 2020). These observations have led to claims that primates respond to death in ways that are similar to humans, by producing strong emotional, social, and exploratory responses (Watson and Matsuzawa 2018; Gonçalves and Carvalho 2019). Among non-human animals, the emphasis on primates may result from easier detection, given the relatively large number of long-term studies, and observations from corvid, elephant, and cetacean species suggest that some understanding of death may be widespread among a wide range of long-lived highly-social species (Gonçalves and Biro 2018; Bercovitch 2020).

Here, we focus on a particularly remarkable behaviour seen in many primates, dead infant carrying by mothers, which in chimpanzees typically occurs for a period of up to three days (Gonçalves and Carvalho 2019). Dead infant carrying (also referred as infant corpse carrying)

is the most frequently reported thanatological behaviour and shows substantial variation in accompanying behaviours across primate species (Fernández-Fueyo et al. 2021), as a result, it offers rich data against which to explore possible explanatory factors. This behaviour has not only been reported in chimpanzees (Matsuzawa 1997; Hosaka et al. 2000; Kooriyama 2009; Biro et al. 2010) but also in bonobos (Fowler and Hohmann 2010; Tokuyama et al. 2017), gorillas (Warren and Williamson 2004; Masi 2020), chacma baboons (Carter et al. 2020), red colobus (Georgiev et al. 2019), geladas (Fashing et al. 2011), ring-tailed lemurs (Nakamichi et al. 1996), bonnet and lion-tailed macaques (Das et al. 2019), Japanese macaques (Sugiyama et al. 2009; Takeshita et al. 2020), marmosets (Thompson et al. 2020), and vervet monkeys (Botting and van de Waal 2020). Several hypotheses have been put forward to explain the function of and motivation for this behaviour (Table 2; for a review see: Watson and Matsuzawa 2018; Gonçalves and Carvalho 2019).

Within an increasingly large field of hypotheses – some of which are mutually non-exclusive – there are some natural groupings based on similarity in the suggested mechanisms or explanations. A first group of hypotheses presumes that primate mothers are unable to understand the ramifications of death and their behavioural responses are simply side effects of evolved physiological mechanisms. Specifically, the 'unawareness hypothesis' states that mothers are unable to discriminate between temporarily unresponsive and irreversibly deceased individuals and simply try to avoid the costs of premature abandonment (Hrdy 1999). The hypothesis predicts that mothers are unable to understand their infants' state and continue providing maternal care (e.g. grooming) and try to elicit responsiveness (e.g. poking, smelling). With increasing time, the ambiguity will dissolve due to the accelerating decomposition of the corpse, which is usually mediated by local climate. A second prediction therefore is that dry and particularly hot or cold conditions favouring mummification should

favour prolonged carrying of dead infants (see also ‘climate hypothesis’: Matsuzawa 1997; Fashing et al. 2011). The ‘post-parturient condition’ hypothesis similarly proposes that the maternal physiological conditions associated with pregnancy and birth favour persistent care of the dead infant as long as the mother is lactating or until resumption of ovulation, for example indicated by sexual swelling (Kaplan 1973). Here, the younger the infant the longer the expected carrying period.

A second kind of hypotheses assumes that primate mothers can have a notion of death, provided they have relevant personal experience. Specifically, the ‘learning about death’ hypothesis states that chimpanzees do not intuitively understand death but can acquire the notion by learning to attend to the relevant cues (Cronin et al. 2011). Here, the predication is that experienced mothers will be aware of the irreversible change and, unlike first-time mothers, should have shorter dead-infant carrying periods. An alternative hypothesis, the ‘grief-management hypothesis’, also assumes that chimpanzees possess a notion of death, and suggests dead-infant carrying represents a consoling strategy to cope with grief. This hypothesis predicts that mothers who are able to carry their dead infants experience lower levels of ‘stress’ hormones (i.e. glucocorticoids) than mothers who could not or did not carry them (Nicolson 1991). A recent study by Girard-Buttoz and colleagues (Girard-Buttoz et al. 2021) reported elevated cortisol levels in infant chimpanzees who lost their mothers, supporting the notion that disruption of the mother-infant bond leads to elevated stress. Similarly, female baboons experience high levels of glucocorticoids when losing an ally to predation and in periods of infanticidal attacks (Engh et al. 2006a, b). Dead infant carrying, therefore, could be a strategy to cope with stress associated with infant loss.

A third group of hypotheses are agnostic about whether chimpanzees possess a notion of death but proposes various adaptive mechanisms that favour post-mortem mothering behaviour. First, the 'learning-to-mother hypothesis' states that dead-infant carrying improves maternal skills (Warren and Williamson 2004), predicting that the behaviour should mainly be observed in inexperienced primiparous females. Second, the 'maternal-bond strength hypothesis' predicts that mothers with older infants share a stronger bond and are thus more likely to show extensive carrying as compared to mothers with younger infants (Watson and Matsuzawa 2018). On the other hand, the 'hormonal hypothesis' states that, after giving birth, the endocrine system of the mother releases hormones (e.g. oxytocin) that stimulate maternal behaviours (Biro et al. 2010). Here, persistent carrying would be the result of a strong mother-infant bond and the younger the infant at time of death the longer the carrying period.

The existence of multiple – sometime contrasting – hypotheses is likely a reflection of the small and highly variable data available and the diversity of potential drivers of this behaviour across different species. A recent systematic study on primates (n=18 species) showed that duration of infant carrying is affected by the age of the mother, with older mothers carrying for longer periods (Das et al. 2019), in contrast with previous findings by Sugiyama and colleagues who found no effect of age (Sugiyama et al., 2009). Infants that died of sickness were carried for longer than those who were stillborn or victims of infanticide, while the age of the infant did not influence duration of carrying (Das et al. 2019). Although dead infant carrying is a shared but rare behaviour in primates, carrying duration seems to be the longest in great apes (Fernández-Fueyo et al. 2021), particularly in chimpanzees (Das et al. 2019). Wild chimpanzees have higher levels of infant mortality compared to captive conspecifics (Courtenay and Santow 1989; Hill et al. 2001), which

provides increased opportunities to observe mothers' responses to their infants' death (Watson and Matsuzawa 2018). Chimpanzee mothers typically carry their dead infants for a few days, though a recent analysis of the largest chimpanzee dataset (n=33 cases) did not provide clear support for any of the previous hypotheses (Lonsdorf et al. 2020). Despite this, it was proposed that the 'unawareness hypothesis' is unlikely because of the presence of atypical carrying postures and sensory cues after death compared to those displayed towards alive infants (Lonsdorf et al. 2020). More recently, a study using the largest primate database to date (n=409 cases and n=50 species) found that dead infant carrying was more likely to occur when the cause of death was non-traumatic and when mothers were younger (Fernández-Fueyo et al. 2021). In addition, the authors showed that carrying duration was greater for younger infants, supporting the importance of the maternal bond. Here, we revisit the discussion on the potential reasons behind dead infant carrying by female chimpanzees with a 40-year dataset of two study groups of the Budongo Forest, Uganda, including three detailed observations of extended dead infant carrying by two different females.

Methods

Study site and subjects

The Budongo Forest Reserve is a semi-deciduous tropical rain forest located along the western Rift Valley in Uganda. This reserve is made of 793 km^2 of protected forest and grassland, including 482 km^2 of continuous forest cover (Eggeling 1947) . The reserve contains a population of approximated 600 East African chimpanzees (*Pan troglodytes schweinfurthii*). Our observations took place in two adjacent communities, Sonso and Waibira, studied regularly by researchers and followed on a daily basis by field assistants since 1990 and 2011 respectively (Reynolds 2005; Samuni et al. 2014).

At the time of the events, the Waibira community contained an estimated 120 individuals, 96 of which could be individually recognised. Individuals involved in the first event were Ketie (KET), a 20-year old adult primiparous female (estimated birth 1998) and her 2-year old female infant Karyo (KYO) born in December 2015. The Sonso community contained 65 named individuals, in addition to three unnamed females in the process of immigrating. The individuals involved in the event were Upesi (UP), a 21-year old parous female (estimated birth 1999) and a) in the second event, her recently born unnamed unsexed infant UP3, born mid-September 2020 and b) in the third event, her 4th born unnamed unsexed infant UP4, estimated birth 7th August 2021. Her first two infants (born in 2017 and 2018) were victims of within-community infanticide before reaching a month old (see Leroux et al. 2021 for one reported case).

In this paragraph we consider the scope for bias in our study subjects by using the STRANGE framework to report potential sampling biases in our study (Webster and Rutz 2020; Rutz and Webster 2021). The Sonso community are of typical size whereas the Waibira community are particularly large as compared to that of other chimpanzees (in a recent comparison of 18 groups across three subspecies: *P.t. schweinfurthii, P.t. troglodytes, P.t. verus*; communities range from 7-144 individuals with a mean 42; within these data the East African sub-species (*P.t. schweinfurthii*) range is 18-144 with a median 49; Wilson et al. 2014). Sonso have a typical female-basied sex ratio among mature individuals (M:F; 1:1.7), whereas the Waibira community have more unusual evenly-balanced sex ratio among mature individuals (M:F; 1:1.2; mean among 9 *P.t. schweinfurthii* communities 1:1.7; Wilson et al. 2014). Of relevance to sampling biases in infant mortality and opportunities to carry dead infants, the Sonso community experience high levels of infanticide (Lowe et al. 2019, 2020). A medium altitude rainforest (~1100m) with significant annual rainfall (~1500mm per year)

the area is slightly more seasonal than true rainforest with a distinct dry-season during December-March and a drier season during June-August (Newton-Fisher 1999).

Ethical note

Data collection was observational and adhered to the International Primatological Society's Code of Best Practice for Field Primatology (MacKinnon et al. 2014). All applicable international, national, and institutional guidelines for the care of animals were followed. Research was conducted under approval by the Uganda Wildlife Authority and the Uganda National Council for Science and Technology. All work was in accordance with the ethical standards of the Budongo Conservation Field Station at which the study was conducted.

Data collection

Researchers and a team of field assistants followed chimpanzees daily (Waibira: from 06:00 to 18:00; Sonso: from 07:00 to 16:30). Long-term data collection included focal individual activity and party composition taken on a 15-min scan basis. In addition, all unusual events or otherwise remarkable behaviour were recorded in detail in logbooks for each community, including births, deaths, and associated descriptions of behaviour (Sonso: since 1993; Waibira: since 2011).

In addition to long-term records, AS, PF, EF, CF, DT and CH together with field-assistants SA, JA, GA, BC, and GM of the Budongo Conservation Field Station observed the extended carry events we report. KET and UP are typically comfortable with the presence of human observers; however, following the death of KETs infant we avoided selecting her as a focal individual because we observed apparent signs of greater than typical arousal (e.g. self-scratching and vigilance) in her interactions with other chimpanzees and we did not want our

extended presence to further impact these. Observations of her behaviour were taken on an ad libitum basis whenever she joined the party of chimpanzees that included a focal individual, but we made an effort to locate and observe her for a brief period of time each day to obtain regular updates on her and her infant's state of decomposition. During the births and deaths of UP's infants, regular research practices had been adjusted due to the Covid19 pandemic. In 2020 activities were restricted to shorter hours of observation (7:30 to 13:00) and limited to CH and the permanent field staff, who focused primarily on health monitoring of the chimpanzees during this period; in late 2021, at the time of UP's second extended infant carry, restricted research activities had resumed. Researchers and field staff opportunistically noted any unusual behaviour exhibited. Particular attention was given to how the bodies, and in one event a potential substitute object, were transported, the response of nearby individuals to the mother or the carcass, the interactions of the mother with the corpse, and the state of the corpse. We were not able to collect physiological samples from either corpse to perform laboratory analyses on the cause of death, nor we were able to retrieve either body for autopsy.

Results

Over a combined 40-year period of observations (30 years Sonso, 10 years Waibira) a total of 191 births were recorded. Of these: 68 (36%) died in infancy (≤ 5 years) offering opportunities for their mothers to carry the infant's corpse post-mortem. We found no evidence for seasonality as deaths (with a confirmed observation month, n=59) occurred throughout the year (Jan n=5; Feb n=2; Mar n=2; April n=3; May n=1; Jun n=3; Jul n=9; Aug n=6; Sep n=10; Oct n=6; Nov n=9; Dec n=3). Of the n=68 infant deaths, we excluded n=3 that died together with their mothers and n=12 because they were partially dismembered or cannibalised during infanticides. Of the remaining n=53 cases, we were able to estimate the

infant's age at death (±1 month) in n=46 cases (87%). The majority (n=25; 54%) died within the first month, n=17 (37%) at 1-month to 1-year old; n=3 (7%) at 1- to 3-years old, and n=1 (2%) at 3- to 5-years old.

We observed n=12 carries of dead infants by their mothers (Table 1), 23% of observed opportunities (n=53). To be included as a case of dead infant carrying we required that the mother be seen with the infant the day after death was estimated to have occurred. In 9 cases the minimum carry length observed was 1-3 days, in 3 cases we observed a longer minimum carry of n=18, n=56, and n= 89 days. These are described in more detail below. The 12 carries occurred in both primiparous (n=1) and multi-parous females (n=11), including a 7th born infant. However, these observations are likely an under-estimate of the frequency of dead infant carrying behaviour in Budongo mothers. In n=36 the mother reappeared alone and could have carried for an unknown period prior to this. In total there were n=29 cases where the mother and dead infant were seen together, of these n=12 included a death with the mother or infanticide with cannibalism. Of the remaining 17 cases, n=12 showed carrying of the dead-infant, a rate of 71%. Of the five cases where the mother was observed with the dead infant but did not carry it, all were infanticides.

Table 1 Carrying of dead infants by Budongo chimpanzee mothers: mother-infant dyads (with the mother first), mother's age, parity (indicated as multi-parous (multi) or primi-parous (primi)), infant's age, cause of death, duration of carrying

Mother-infant	Age mother (years)	Parity	Age infant (months)	Cause of death	Minimum carrying duration (days)
KG-KG2	21 ±3	multi	0.03	still birth (suspected)	2
ML-ML2	26 ±3	multi	0.03	still birth (suspected)	1

JN-JN2	21 ±1	multi	0.5	unknown	1
ZM-ZM6	41 ±5	multi	0.4	unknown	1
JN-JN4	28 ±1	multi	0.25	infanticide	3
KU-KU5	34 ±3	multi	0.1	infanticide (suspected)	2
KL-KL7	34 ±1	multi	0.12	infanticide	2
ML-ML5	39 ±5	multi	0.06	infanticide (suspected)	3
KET-KYO	20 ±1	primi	25	respiratory infection (inferred)	18
KU-KU7	40 ±3	multi	0.15	unknown	2
UP-UP3	21 ±1	multi	0.25	unknown	56
UP-UP4	22 ±1	multi	0.25	unknown	89

Extended dead infant carrying

A detailed description and videos of the observations are available in the Supplementary Materials. Here we provide a summary of the key information..

Observation 1: KET, extended dead infant carrying in Waibira

KET's first born infant KYO was last seen alive on the 6th of January 2018, aged 25 months. On the 7th of January 2018 KET was observed carrying KYO who appeared lifeless. Other chimpanzees were present and were apparently aware of her arrival with the infant but showed no atypical reactions to KET or the corpse. The likely cause of death was inferred to be respiratory infection. During the first day KET was observed scratching herself repeatedly before approaching a water area and when sitting close to a sub-adult male. These scratches appeared to be a sign of arousal (fast and repeated, and not accompanied by grooming or response waiting). On several occasions she moved her hand over the dead body apparently to chase away the flies. Other than this, during the entire 18-day period, she was never observed to provide any direct maternal care (grooming, inspecting, touching, or peering)

other than carrying, and regularly left the body at short distances (up to 4m) without visually monitoring it. She did not stop others from approaching herself or the dead infant. When moving or feeding in a tree, the dead body was usually (15 out of 16 observations) placed in her right leg pocket, when on the ground she carried the body in her hand or arm (see Online Resources). On one occasion a nulliparous young adult female (MON) was observed to briefly carry the corpse in one hand while KET followed her. Across the 18-days KYO's corpse decomposed, initially increasing in smell. By the 4th day, no hair remained on the body. By the 9th day, the body looked "dried". By the 10th day the pungent smell and number of flies decreased. It is likely that at this stage the body was completely mummified. No other chimpanzees responded noticeably to either the smell or the flies. On the last day of observed carrying, the body was still intact with only eyes missing and one deformed ear.

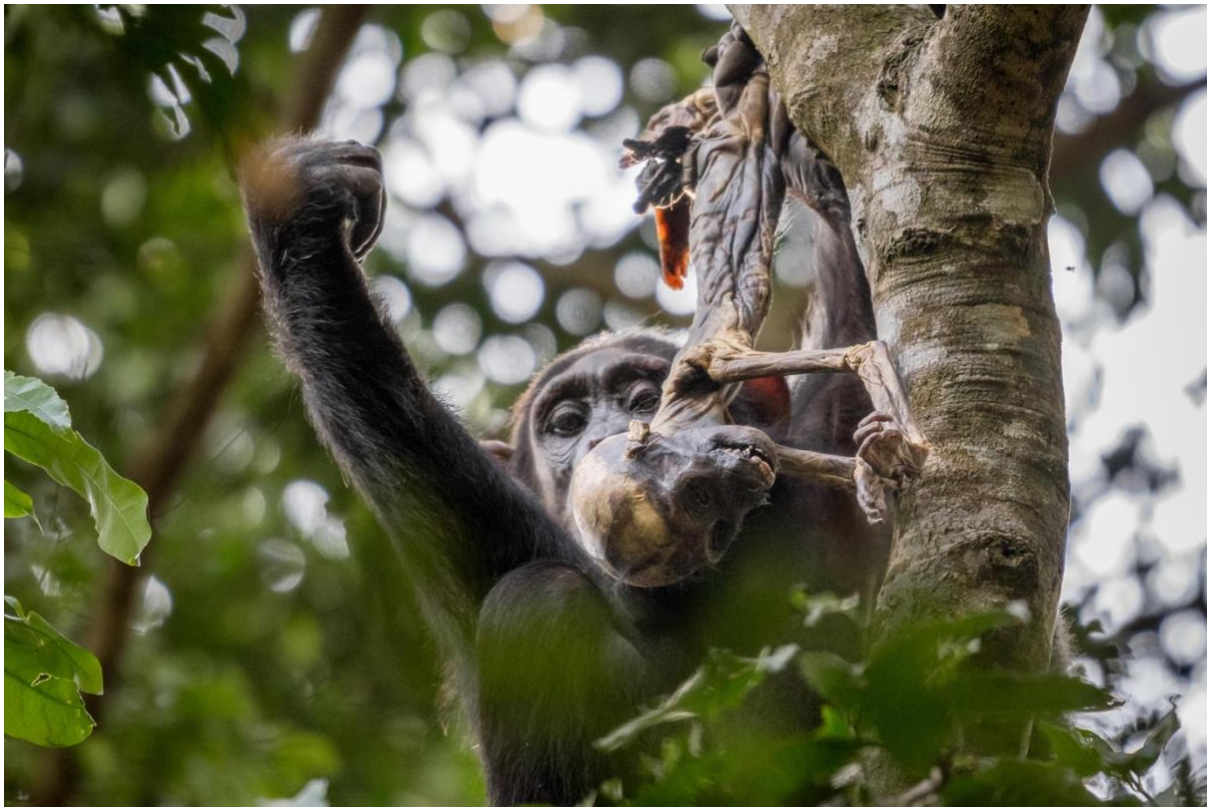

Fig. 1 KET holding KYO's mummified body while sitting on a tree (picture taken by AS on the 21.01.2018)

Observation 2: UP, extended dead infant and substitute object carrying in Sonso

UP was first seen on the 25th September 2020 with an apparently recently dead infant (UP3), estimated to be 1-week old. Her two previous infants were killed by intra-community infanticide when under 2-weeks old. While some immature individuals (< 10 years old) inspected the carcass, no others did, and an adult male showed no interest even while grooming UP. The infant's corpse had started to dry out, but had a noticeable smell and flies, and was assumed to have died several days earlier. UP was observed on the 4th and 26th of October and the 8th and 19th of November, carrying the corpse on all occasions. She held it in her hand when on the ground and moved it to a leg pocket when climbing or moving in trees. By the 8th November the corpse appeared fully mummified. UP was last seen with the corpse on the 19th November, a minimum carry duration of 56-days (although likely several days longer given corpse appeared partially dry on first observation). She was next seen on the 23rd November. When approaching a water hole at the base of a tree, she carried a twig ~50cm long in her mouth. As she reached the hole she transferred the twig to her hand and left leg pocket, drank, and then returned it to her mouth (see Online Resources). She continued to carry the twig throughout the morning, including while climbing large trees, and when patrolling with the group over several kilometres. She was seen on the 24th November, and 3rd and 4th December, and was again observed to be carrying a similar twig consistently. She was not seen to put it down on the ground. She was seen briefly on the 5th December, but it was not clear if she had a twig with her, and when she was next observed in the new year (30th January) she no longer carried anything.

Observation 3: UP, 2nd extended dead infant carrying in Sonso

UP was first seen on the 28th August 2021 with another dead infant (UP4), estimated to be 1-week old. The infant's corpse had started to dry out but had a strong smell and on the 30th of

August flies could be seen hovering around it. Given that the corpse still had a strong smell but was already partially dried, it was assumed to have died at least one week prior. The cause of death was unclear; however, UP was observed with wounds on her head and on her left arm. UP was observed using three main carrying styles when traveling on the ground or moving in trees. She either carried the corpse in one hand (typically left one), in the mouth, or in one leg pocket (typically left one) (see Online Resources). When resting, she placed the corpse on her lap, in a leg pocket, held it in one hand, or placed it on the ground close to her. UP was not observed providing direct maternal care (e.g. grooming, inspecting, or peering) to the corpse, though she was observed moving her hand around the dead body to chase away flies on several occasions. On one instance UP was victim of aggression from other females during which she dropped the corpse, and then followed the group when traveling and left the corpse behind. Soon after, she was observed returning to retrieve the corpse. We observed a juvenile male orphan (KJ) following her and peering close to the corpse on a few occasions. No other individual was observed taking interest in or showing response to the corpse. Throughout the observation period, UP was often seen in large groups and regularly socialising with adult males (e.g. grooming). On this occasion there were no observations of object carrying. UP was seen carrying the corpse on: the 28th, 30th and 31st of August; the 2nd, 6th, 8th, 9th, 11th, 13th, 14th, 16th, 18th-23rd,24th, 25th and 29th of September; the 7th, 12th, 13th, 15th-21st, 26th, 28th of October; and the 3rd, 10th, 14th and 17th of November. On the 18th of November she was seen without the corpse and had resumed her sexual cycle (with visible sexual swelling) for the first time since the last pregnancy.

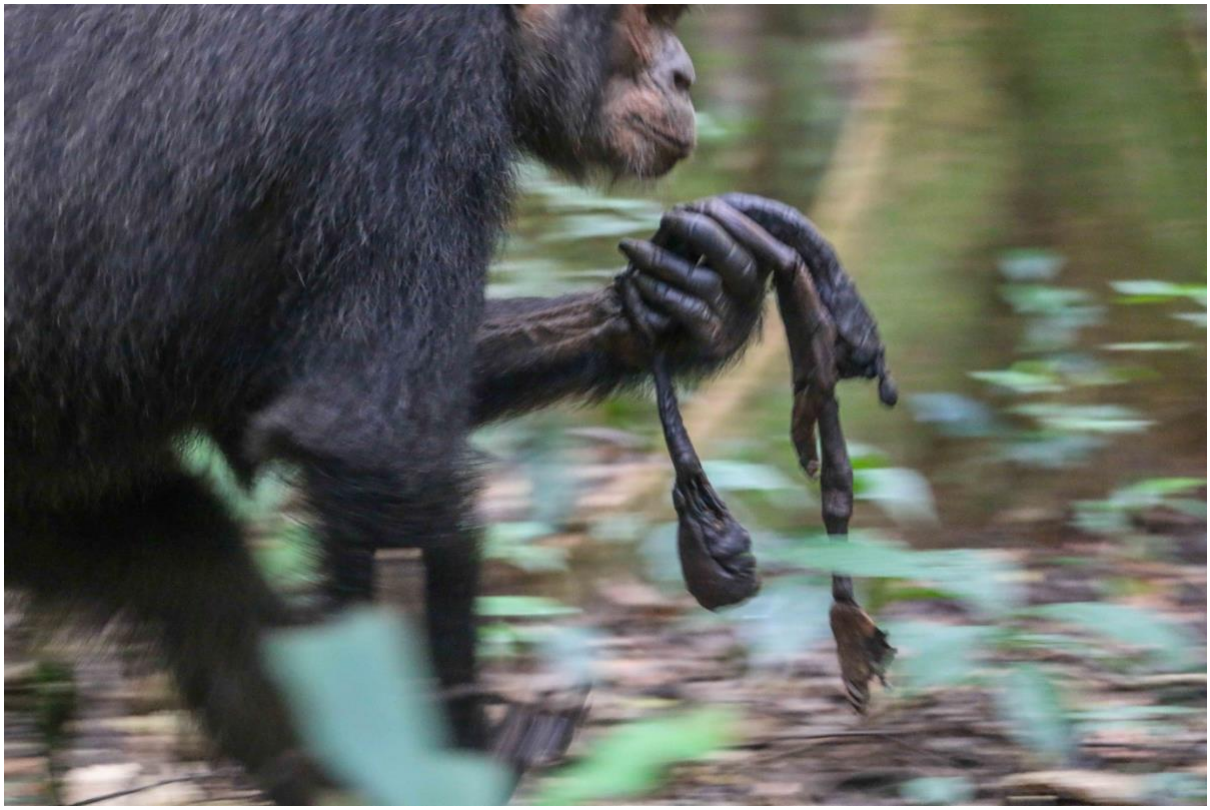

Fig. 2 UP carrying UP4's mummified body in her hand while traveling on the ground (picture taken by EF on the 30.08.2021)

Discussion

Human responses to deceased conspecifics are remarkable. Despite the fact that dead individuals have lost all biological importance in terms of kinship, reproduction, or cooperation, humans do not immediately abandon their dead but exhibit a plethora of post-mortem social behaviour towards them, including social gatherings, physical tending, and various burial practices (Parkes et al. 1997). These activities can last for days but are typically terminated by the onset of physical decay, though certain cultures continue to interact with the deceased afterwards (e.g. Hollan 1995). There is archaeological evidence that tending the dead evolved before modern humans (Martinón-Torres et al. 2021), with burials now documented in *Homo sapiens neanderthalensis* (Rendu et al. 2014) and *Homo*

naledi (Dirks et al. 2015), and interpreted as an indication of some abstract notion of death and understanding of irreversible loss (Pettitt 2018).

What do great apes experience, cognitively and emotionally, when losing a socially close individual? In this study we compiled long-term data on chimpanzee mothers that had lost their infants but continued carrying them for days, raising questions about evolutionary continuity in the function of this behaviour and the cognition of understanding death. Dead-infant carrying was practiced by both parous and primiparous mothers with both new-born and older infants. It occurred in at least a fifth, but more likely in almost three quarters of cases (if we consider only those cases in which we were able to observe the mother immediately after the infant's death). As compared to other chimpanzee communities even this value may be an under-estimate of the frequency with which bereaved female chimpanzees carry their infants. The Sonso community, in which we made most of our observations, experiences periodic high levels of infanticide (Lowe et al. 2020). These infanticide cases are often accompanied by some level of cannibalism or dismemberment, and/or the infant is taken from the mother (Lowe et al. 2019), which may limit or shorten mothers' opportunities to carry (Gonçalves and Carvalho 2019; Fernández-Fueyo et al. 2021).

We found no seasonal or infant age effect on dead infant carrying. We also reported three prolonged cases of extended infant carrying. Our observations suggest that these mothers, despite the evidence of irreversible loss including absence of any resemblance to living infants, continued to experience a strong attachment to their deceased infants. Neither female had any other living offspring and one, after eventually abandoning her dead infant after 56 days, replaced the corpse with a twig, which she carried for at least another two weeks. In our

cases dead-infant carrying was not accompanied by other forms of maternal care, such as grooming or other forms of maternal attention or interactions, which sometimes occurs very early after an infant's death (Matsuzawa 1997; Biro 2011), suggesting that the two mothers had become aware of the biological facts. Both mothers were forced to use atypical modes of infant carrying, including mouth carrying, more typically used for objects (Lonsdorf et al. 2020), as live infants cling to the back or belly of their mothers during travel. Also relevant is that, unlike other groups of animals, chimpanzees do not often cannibalise their own dead infants (but see Fedurek et al. 2020 for two exceptions). Overall, these data suggest that the 'unawareness hypothesis' is an unlikely explanation of chimpanzee behaviour towards dead conspecifics.

As neither mother appeared to inspect or interact with the infant beyond carrying, our observations do not support the 'learning about death' hypothesis, although maternal social behaviour has been seen in other chimpanzee mothers during the initial stages after death (Matsuzawa 1997; Biro et al. 2010). Similarly, we did not find general support for the 'learning to mother hypothesis'. While both KET and UP were inexperienced mothers (primiparous or parous but all offspring killed at under a month old),10 of the 11 mothers who carried their dead infants were parous and two of these cases were with 6th and 7th born infants. Cases of extended carrying by parous mothers in other groups also suggest limited support the 'learning to mother hypothesis' (Matsuzawa 1997; Biro et al. 2010; Biro 2011; Lonsdorf et al. 2020). However, in line with the fact that younger mothers carry dead infants for longer (Fernández-Fueyo et al. 2021), our observations would fit a suggestion that rare instances of particularly extended carrying across several months might occur when mothers have limited mothering experience.

Because we did not collect any hormonal data to assess the levels of stress associated with this event, we were unable to evaluate the 'grief-management hypothesis' or the 'hormonal hypothesis'. However, the fact that elevated glucocorticoid levels have been reported in chimpanzees and baboons following the death of a socially important group member strongly suggests that these would also be present for chimpanzee mothers in these instances given that the bond they share with their infants is among their most significant, with typically 3-5 years before weaning, and often up to 10-years of daily close contact (Pusey 1983; Lonsdorf and Ross 2012; Stanton et al. 2017).

Our observations provide more mixed support for other hypotheses. One observation took place during the peak of the driest season of the year, whereas the other two took place during the wettest season of the year. Thus, rather than mummification being the result of favourable climactic conditions, it is possible mummification was observed because the extended carrying durations allowed for it. Recent explorations of several large datasets also found no support for the 'climate hypothesis' (Das et al. 2019; Lonsdorf et al. 2020; Fernández-Fueyo et al. 2021). The evidence for the 'post-parturient condition hypothesis' is similarly mixed; of the three extended carries two infants were new-born, while the other was 2-years old. The longest carry reported was for a new-born; however, other new-born infants were carried for short periods of just a few days. One of the three extended carries terminated with the resumption of the mother's reproductive cycles. Our data do not provide straightforward support for the 'hormonal hypothesis' – the extended carrying by KET of her 2-year old would fit this pattern; however, the extended carrying by UP of her two new-borns do not. Other observations of non-mothers carrying dead infants suggest that the hormonal hypothesis cannot explain observed extended carrying alone (Watson and Matsuzawa 2018; Masi 2020). However, hormonal data (that could potentially also show abnormal hormonal

production in either of the two females) are needed to investigate this hypothesis effectively. While the same argument may apply to the 'maternal-bond strength hypothesis', with KYO's case providing support and UP's cases providing counterevidence, it may be worth noting that these were UP's third and fourth infants in a five-year period, the first two having been killed at under a month old in within-community infanticides (one suspected, one confirmed). As a result, it may be difficult to assess the nature of her bond with these infants. Her apparent use of a 'substitute' in her carrying of a twig together with the even more prolonged second carry suggest she had a particularly strong motivation to carry. These observations, combined with the fact that all recorded instances of carrying in our dataset concern infants who died before weaning age, indicate that maternal behaviours, which are not limited to maternal care, likely play an important role (Fernández-Fueyo et al. 2021).

Table 2 Hypotheses, predictions, and supporting evidence from the present study for dead infant carrying

Hypothesis	Prediction	Study support
Unawareness	Dead infants are treated as alive.	Unlikely
Post-parturition	Younger infants are carried for longer.	Mixed
Learning about death	Mothers inspect and check state of infant.	Unlikely
Grief-management	Stress levels are lower in mothers carrying dead infants.	Not tested
Learning-to-mother	Primiparous mothers carry dead infants more often/for longer.	Unlikely
Maternal-bond strength	Older infants are carried for longer.	Mixed
Hormonal	Strongly bonded and older infants are carried for longer.	Not tested-Mixed

Within the detailed observations of longer carries, there were two examples of particularly rare behaviour: KET allowing MON to carry KYO, and UP's stick carrying. Carrying the infant of others over periods of time longer than one day is an extremely unusual behaviour in primates, though it has been observed on two occasions in Budongo: adult males snatched new born infants and carried them still alive for at least two days (in one case the male continued to carry the infant for a further two days after its death; Notman and Munn 2003; unpublished long-term data) and was suspected in another case where a daughter was observed carrying her mother's new infant for several days without the mother being present (unpublished long-term data). It is possible that KET tolerated MON's behaviour because of a close bond the two shared, another explanation is that her own bond with the infant's body apparently had decreased by the 13th day.

We are not aware of any other reports of primate mothers carrying substitute objects following their infant's death and we are cautious about interpreting this observation. Chimpanzees may carry objects, including twigs, for many reasons; however, a number of features suggest that this was related to UP's infant carrying. Prior to the incident, neither UP nor any other adult Budongo chimpanzees had ever been observed to carry non-food objects between locations. They are notoriously non-stick-tool users (Whiten et al. 1999; Gruber et al. 2011), with a substantial literature suggesting that this is both absent, and robust to scaffolding of its acquisition (Gruber et al. 2009; Gruber 2016). Chimpanzees have been reported at several sites to engage in 'doll' play, where substitute objects, including logs and sticks, are carried as if they were a young infant (Matsuzawa 1997; Kahlenberg and Wrangham 2010). This behaviour typically peaks in juveniles and is more frequent in females and while it is observed in some adult females it ceased once they became mothers (Kahlenberg and Wrangham 2010). The description of log doll use in Bossou is of particular

interest here, as it was carried by a juvenile female during the period that her mother was carrying her sick infant sister, who subsequently died and whose body was also then carried (Matsuzawa 1997). UP's behaviour was observed multiple times over several weeks. Unlike the descriptions of other 'dolls' she was not seen to play with or interact with the object, treating it instead in the same way as she had her infant's corpse. Thus, in addition to object-carrying being associated with the absence of infants in nulliparous mothers, it may also be associated with the loss of an infant in bereaved mothers. In humans, the use of transitional objects has been suggested to function as a coping mechanism for grief following a bereavement (Lister et al. 2008).

To sum up, our observations are consistent with previous observations that chimpanzee mothers respond to the death of their infants with carrying behaviour across communities. Furthermore, our observations support the argument that these mothers act as if they are aware of the loss but are continuing to display a strong attachment to the bodies of their infants and may be affected by psychological processes akin to human grieving. Nevertheless, more detailed hormonal data are needed for a test of this potential mechanism. A combination of ecological conditions favouring mummification, and social factors, such as the strong bond shared between mothers and their infants, may explain the three particularly extended carries by Budongo chimpanzees. While we did not observe other indications of maternal care in these cases, we are cautious about interpreting this as a wider absence in Budongo mothers. Mothers' pattern of behavioural responses to death may be individually specific and nuanced, resulting from a combination of physical, ecological, and psychological factors, and many more observations are needed to generalise at the population or species level. Our interpretations are limited by the small dataset and the large number of competing and non-mutually exclusive hypotheses, and we encourage researchers and long-term field

sites to continue to report the rare behaviours observed in different populations, for example by contributing to open-access databases such as 'ThanatoBase' (http://thanatobase.mystrikingly.com), to allow a richer exploration and more robust hypothesis testing of non-human primates' reaction to death.

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