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# Death Among Primates: A critical review of non-human primate interactions towards their dead and dying

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# Death among primates: a critical review of non-human primate interactions towards their dead and dying

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ABSTRACT

For the past two centuries, non-human primates have been reported to inspect, protect, retrieve, carry or drag the dead bodies of their conspecifics and, for nearly the same amount of time, sparse scientific attention has been paid to such behaviours. Given that there exists a considerable gap in the fossil and archaeological record concerning how early hominins might have interacted with their dead, extant primates may provide valuable insight into how and in which contexts thanatological behaviours would have occurred. First, we outline a comprehensive history of comparative thanatology in non-human primates, from the earliest accounts to the present, uncovering the interpretations of previous researchers and their contributions to the field of primate thanatology. Many of the typical behavioural patterns towards the dead seen in the past are consistent with those observed today. Second, we review recent evidence of thanatological responses and organise it into distinct terminologies: direct interactions (physical contact with the corpse) and secondary interactions (guarding the corpse, vigils and visitations). Third, we provide a critical evaluation regarding the form and function of the behavioural and emotional aspects of these responses towards infants and adults, also comparing them with non-conspecifics. We suggest that thanatological interactions: promote a faster re-categorisation from living to dead, decrease costly vigilant/caregiving behaviours, are crucial to the management of grieving responses, update position in the group's hierarchy, and accelerate the formation of new social bonds. Fourth, we propose an integrated model of Life-Death Awareness, whereupon neural circuitry dedicated towards detecting life, i.e. the agency system (animate agency, intentional agency, mentalistic agency) works with a corresponding system that interacts with it on a decision-making level (animate/inanimate distinction, living/dead discrimination, death awareness). Theoretically, both systems are governed by specific cognitive mechanisms (perceptual categories, associative concepts and high-order reasoning, respectively). Fifth, we present an evolutionary timeline from rudimentary thanatological responses likely occurring in earlier non-human primates during the Eocene to the more elaborate mortuary practices attributed to genus *Homo* throughout the Pleistocene. Finally, we discuss the importance of detailed reports on primate thanatology and propose several empirical avenues to shed further light on this topic. This review expands and builds upon previous attempts to evaluate the body of knowledge on this subject, providing an integrative perspective and bringing together different fields of research to detail the evolutionary, sensory/cognitive, developmental and historical/archaeological aspects of primate thanatology. Considering all these findings and given their cognitive abilities, we argue that non-human primates are capable of an implicit awareness of death.

*Key words*: comparative thanatology, epimeletic behaviour, deceased infant carrying, deceased conspecific, concept of mortality, grief.

CONTENTS

## I. INTRODUCTION

Primate thanatology is the scientific study of the phenomenon of death and dying in non-human primates, including the physiological, behavioural, social and psychological processes associated with it (Anderson, 2017). Because non-human primates (henceforth primates) occupy a close evolutionary trajectory to humans, they remain the best candidates to investigate how our ancestors before the *Homo* lineage might have responded to death, preceding the emergence of ritualised behaviours towards the dead – one of the defining traits of our species.

Where recognising a corpse is evolutionarily advantageous for a species, natural selection will act on it. Several species in the animal kingdom (eusocial insects, fishes and rodents) exhibit either/both necrophoric or necrophobic behaviours towards dead conspecifics. Such reflexive actions may be tied to predator evasion or pathogen avoidance mechanisms and are mostly triggered *via* chemoreception or olfaction (Gonçalves & Biro, 2018). Primates, however, unlike some animals guided primarily by olfaction, move in a multimodal realm, relying heavily on sight and sound, among other senses, to form an accurate perception of their environment (Ghazanfar & Santos, 2004). In this regard, it is not surprising that they show a diverse range of thanatological behaviours, from emotional ambiguity to exploratory actions that rather set them apart from the less-flexible responses exhibited by other animals, which serve as an active way of gathering novel information about the corpse and the contextual cues that surround it – behavioural trends they share with corvids, proboscids and cetaceans (Gonçalves & Biro, 2018).

Although the number of publications has been increasing (Fig. 1) and serious attempts to review these records have been carried out, they have either confined themselves to chimpanzees (Pettitt, 2011; Hanamura, Kooriyama & Hosaka, 2015), integrated non-primate species with the primate data (Piel & Stewart, 2015; Anderson, 2016), and/or focused on particular aspects such as grief (Pollock, 1961; Averill, 1968; Zeller, 1991; King, 2013); only a few have attempted to synthesise the available primate thanatological data (Box, 1984; Vieira, 1987; Anderson, 2011). Here, we not only discuss new developments in the field, but also look back at the first observations, offering a comprehensive and updated outlook of the death phenomenon among primates and proposing future directions for the emerging field of primate thanatology.

## II – PRIMATE THANATOLOGY: A SCATTERED HISTORY

### (1) Early observations

The early 19th century was a period of great intellectual transformation. Europe witnessed the rise of the first modern zoological gardens and natural history museums, the latter featuring wild specimens brought back from colonial territories (Hoage & Deiss, 1996; Burkhardt, 1999). In Paris at the *Jardin des Plantes*, Fréderic Cuvier was head of the *Menagerie*, where he kept living animals in confinement, believing them to be useful learning tools, akin to the dead animals in museums. These first attempts at keeping live animals were only partially successful as many died from disease or the harsher climate (Baratay & Hardouin-Fugier, 2003). Such was likely the fate of a common marmoset (*Callithrix jacchus*) whose bereaved companion Cuvier described as inconsolable before himself succumbing to death (Cuvier *in* Houzeau, 1872). Whilst travelling in India, James Forbes (1813) reported the shooting of a female monkey and described how the troop responded by surrounding the gunman and advancing in a "menacing posture", mentioning one particular male that "stood his ground, chattering and menacing in a furious manner" before beginning a "lamentable moaning" and seeming to "beg" for the body (Forbes, 1813, p.17).

It was with Charles Darwin that the notion of continuity between man and other animals gained scientific credibility – although, despite musing over the possibility of other animals' understanding of death, he credited only humans with an awareness of their own mortality (Darwin, 1871). Turning to something he could measure, Darwin published his writings about the field of emotion, thoroughly detailing the mechanics of weeping, associating them with depressive states, and in so doing, linking the biological underpinnings of grief (Darwin, 1872). Arthur Brown (1879) published a report on a captive male chimpanzee's (*Pan troglodytes*) behaviour following the death of its female "cagemate" – attempting to rouse the corpse, crying, and then whimpering. Richard Garner, in his endeavour to unlock the language of apes, witnessed two chimpanzees he had acquired die of illness and, through the reactions of the living ones, proposed that they must have an understanding of death (Garner, 1900).

Through a comprehensive reading of these pre-ethological reports spanning from the 19th to the early 20th centuries, we find three main patterns concerning primate behaviours towards their dead: (1) carrying/dragging corpses (Bowdich, 1819; Mollien, 1820; Kipling, 1891; Loveridge, 1923); (2) mobbing/defending corpses from attackers (Forbes, 1813; Johnston, 1885; Jenks, 1911; Reichenow, 1920; Aschemeier, 1921); and (3) apparent grieving over deceased companions (Houzeau, 1872; Brown, 1879; Sheak, 1917; Burbridge, 1928; Coolidge, 1933).

Although anecdotal and tinged with naïve anthropomorphism, these reports rather accurately describe behavioural patterns that are recurrent in present-day observations.

### (2) Educated insights: Yerkes, Marais and Zuckerman

At the beginning of the 20th century, a second wave of accounts is characterised by detailed reports from two intellectual descendants of Darwin: Robert Yerkes and Solly Zuckerman. Yerkes reported the behaviour of a female rhesus macaque (*Macaca mulatta*) that kept her dead infant for an extended period, interpreted as a manifestation of maternal instinct (Yerkes, 1915). Later, Yerkes and his wife described the cognitive and emotional aspects of apes, writing on the subject of grief and depression: it was "beyond dispute" that chimpanzees underwent such emotional states (Yerkes & Yerkes, 1929).

Eugène Marais, renowned for his pioneering field studies with chacma baboons (*Papio h. ursinus*), described the behaviour of a captive female whose infant had been severely injured and removed for treatment. She exhibited signs of distress, called continuously, and rarely ate for the duration of her infant's absence. When the dead infant was presented to her, she gave calls, touched and sniffed it, but made no protest upon its removal, seemingly implying "a comprehension of the significance of death and its consequence" (Marais, 1969, p.125).

Zuckerman (1932) had a more conservative opinion. During his residence at London Zoo, he observed a staggering number of violent interactions among hamadryas baboons (*Papio hamadryas*), with more than two thirds of the troop dying from stress or injuries during a six and a half year period and only one infant surviving out of the 15 that were born. Anticipating the research of Harry Harlow, he spoke of an indiscriminate "reaction to fur" that orphaned baboon infants showed, clinging to their mother's fur after her death and being equally soothed by the carcass of another dead baboon. Females were observed carrying their dead infants for days and group members were fiercely opposed to the removal of a companion's corpse. Males were also observed copulating with female corpses. In Zuckerman's view, that they would show these behaviours regardless of whether the individual was alive, wounded or dead, was an indication of their lack of awareness of death (Zuckerman, 1932).

It is important to state that these observations were made in less than ideal captive settings. In Yerkes's case, the rhesus monkey was kept in a small cage that might have accounted for an uncharacteristically long carrying period. Zuckerman's observations were made within an artificial population of individuals, during an event now dubbed the "Monkey Hill Massacre", resulting from a lack of knowledge of Hamadryas baboon social organisation (Zuckerman, 1932). Similar miscalculations led to a violent reorganisation within the introduced rhesus group on Cayo Santiago, Costa Rica (Carpenter, 1959).

### (3) Initial field reports

Most reports from the field took the form of side notes to larger research agendas (Kawai, 1960; Booth, 1962; Jay, 1962; Schaller, 1963; DeVore, 1963; Koford, 1965; Bernstein, 1968; Struhsaker, 1971; Mittermeier, 1973), with notable exceptions (Teleki, 1973; Nash, 1974; Mohnot, 1980). Jane Goodall described several chimpanzee reactions towards dead and dying conspecifics, many occurring during an outbreak of Polio (van Lawick-Goodall, 1968, 1971; Goodall, 1986). One female (Olly) started carrying her infant in unusual fashions (slung over her shoulder, by the arm or leg) once he stopped showing signs of life, whilst in marked contrast another female (Mandy) still carried her dead infant ventrally. Goodall noted their "dazed" expressions (van Lawick-Goodall, 1968), later commenting on their possible awareness of their infant's deaths (van Lawick-Goodall, 1971). There were also reports of an adult female (Honey Bee) caring for her fatally injured mother, and the grief-like reaction of a juvenile (Flint) to the death of his mother (Flo), himself dying days later (Goodall, 1986).

Despite some authors arguing that such behaviour was non-adaptive, others speculated that it may be evolutionarily advantageous, particularly for mothers carrying temporarily immobilised infants – a behaviour proposed to be selected for in species with low reproductive rates, such as primates (Alley, 1980).

### (4) Experimental/quasi-experimental research

The emerging subfield of primate thanatology was not outside the experimental sphere. Besides key studies exploring grief-like responses using the *infant-mother separation paradigm* (Jensen & Tollman, 1962; Seay, Hansen & Harlow, 1962; Hinde, Spencer-Booth & Bruce, 1966; Kaufman & Rosenblum, 1967), other experimental paradigms included: the *stuffed/fresh corpse paradigm* (Hebb, 1946; Butler, 1964, Bertrand, 1969; Kaplan, 1973), where a recently dead/stuffed primate was introduced to the group; the *anaesthesia paradigm* (Rosenblum & Youngstein, 1974; Rosenson, 1977; Negayama, 1988), involving the presentation of a live but temporarily inert individual; the *playback call paradigm* (Allen & Hauser, 1991; Palombit, Seyfarth & Cheney, 1997), whereby calls of dead infants or their mothers are played to group members; and the *hormonal paradigm* (Engh *et al*., 2006; Kaplan, Pines & Rogers, 2012; Seyfarth & Cheney, 2013), which measures stress levels through sample collection upon the death of a group member.

The American Sign Language (ASL) projects with great apes that emerged in the 1970s also contributed to our knowledge of primate thanatology. Despite no formal tests being done with regards to communicating concepts of mortality, and the available data on this matter remaining anecdotal, attempts by researchers to communicate about death for both for the western lowland gorilla (*Gorilla g. gorilla*), Koko (Patterson & Gordon, 1993), and the chimpanzee, Washoe (Fouts & Mills, 1997), had inconclusive results. Koko, when she was seven, was asked a series of questions relating to death, such as when do gorillas die, to which she signed "Trouble, old", where do they go after death, signing "Comfortable Hole Bye", and how they feel upon death, signing "Sleep". When told that her cat was killed by a speeding car she "cried"; three days after she was questioned again about the cat, signing "Sleep". On one occasion she saw a picture of a similar cat pointing and signing to it "Cry, Sad, Frown" (Patterson & Gordon, 1993, p.64). A second case involves, Washoe, whose infant had died. Immediately after being told the news, Washoe dropped her cradling arms and "moved over to a far corner and looked away her eyes vacant" (Fouts & Mills, 1997, p.224).

Others did not follow this line of inquiry, such as David Premack, renowned for his research in chimpanzee cognition, who stated: "Until I can suggest concrete steps in teaching the concept of death without fear I have no intention of imparting the knowledge of mortality to the ape" (Premack, 1976, p.674). Gordon Gallup, whose insightful experiments with mirror recognition suggested that great apes possess an awareness of self, claimed that apes could very well also have an awareness of death (Gallup, 1979, 1998).

### (5) Current views

Published accounts on primate thanatology have been increasing in number (Fig. 1). Recent decades have yielded reports from Japanese (Negayama, 1988; Kano, 1992; Yoshida, 1994; Nakamichi, Koyama & Jolly, 1996; Matsuzawa, 1997; Hosaka *et al*., 2000; Kooriyama, 2009; Sugiyama *et al*., 2009), Chinese (Lu, Zhao & Li, 2007; Chen & Li, 2011; Li *et al*., 2012;

Chai *et al*., 2013; Yang, Anderson & Li, 2016; Guo *et al*., 2016) and Indian (Rajpurohit, 1997; Balasubramanian & Sabu-Jahas, 1997; Gupta, 2000; Sharma *et al*., 2011) primatologists, in a field previously dominated by British and American researchers.

If ever a picture was worth a thousand words, then certainly the image printed in the November 2009 edition of National Geographic Magazine showing a dead chimpanzee being carried away in full view of her silent community members was the case (Speede, 2013). The story renewed interest in the matter of death awareness in non-human animals. Soon after, key papers published on the subject (Anderson, Gillies & Lock, 2010; Biro *et al*., 2010; Fashing *et al*., 2011; Cronin *et al*., 2011) sparked both curiosity and controversy – particularly Anderson *et al*. (2010) whose claims that the chimpanzees were checking for signs of life and possibly attempting to resuscitate their deceased group member were met with criticism and termed anthropomorphic (Semple *et al*., 2010; Penn, 2011), as well as inciting recommendations of cautious interpretation (Barrett, 2012). Over the years, many scholars have given credence to the possibility of chimpanzees having an awareness of death (de Waal, 1996, 2013; Gallup, 1998; Bering, 2001; Boesch, 2012). Conversely, because they greet each other but do not communicate goodbyes, it has been contended that, at a profound cognitive level, they may lack awareness of mortality (McGrew & Baehren, 2016).

However, these statements currently stand on the confines of uncontrolled observation, with its strengths and limitations, on a phenomenon that is ultimately rarely witnessed in long-lived animals. As claimed by Bering, “ethological reports must — for now — suffice as our only window through which to glimpse this very interesting topic. But it is a window with a good view.” (Bering, 2001, p.124).

## III. PRIMATE THANATOLOGY: CONTEMPORARY REPORTS

### (1) Dead infants

Females of several primate species have been observed persistently to carry their deceased infants (sometimes for prolonged periods of 10 days or more), regardless of the circumstances that caused the fatality (Fig. 2). Other recorded behaviours include grooming, swatting flies away from the corpse and sometimes even consuming part of it. Primatologists have described their expressions as “puzzled”, “confused” or “dazed”, which raises the question as to whether they have some, if any, understanding of death.

These behaviours are striking because they seem maladaptive. Whilst live infants are energetically costly to the mothers who carry them, ultimately they increase reproductive fitness – something a dead immature offspring cannot do. Holding a lifeless corpse hinders locomotion, negatively impacting foraging and predator avoidance. Some will solve these difficulties by adopting a tripedal gait, carrying the corpse ventrally, using the neck and shoulder to wedge it, drag it along the ground, or even carry it dorsally using the tail as an extra limb. While some hypotheses have been proposed to explain post-mortem carrying (Table 1), it is still a matter of debate which one offers the most powerful explanation. Because some are mutually non-exclusive it is likely that many factors, depending on context, contribute to these behaviours (see Watson & Matsuzawa, 2018).

### (*a*) *Mother–infant dynamics*

Dead-infant carrying is the most prevalent thanatological behaviour distributed in several primate taxa (Fig. 3). This should not be surprising since: (1) primates follow a typical trend observed in many vertebrate species of high infant mortality (Bronikowski *et al*., 2011); and (2) unlike adolescents and adults who are abandoned at their site of death, dead infants and juveniles are usually carried by the mother for longer durations, allowing easier detection. Nevertheless, the mother will, invariably, cease to carry the corpse, leaving it unattended for progressively longer periods until finally abandoning it (Jay, 1962; Nash, 1974; Green, 1975; Altmann, 1980; Hosaka *et al*., 2000; Cronin *et al*., 2011).

Many authors have claimed that the mother ceases to treat her infant as a live one during this period – carrying it in awkward positions, by the leg or tail, upside down, using the mouth or dragging the corpse along the ground (van Lawick-Goodall, 1968; Green, 1975; Altmann, 1980; Lu *et al*., 2007; Perry & Manson, 2009; Biro *et al*., 2010; Fashing *et al*., 2011). Green (1975), who conducted a comprehensive vocal study with wild Japanese macaques (*Macaca fuscata*), noted that mothers gave out particular vocalisations when their infants died, repeated whilst carrying the infant or distant from it. Some have proposed that infantile colouration may elicit *post-mortem* carrying (Jay, 1962; Alley, 1980; Rajpurohit, 1997), but this does not explain why such behaviour occurs in females from myriad primate species – some with flamboyant natal coats and others non-conspicuous.

Perry & Manson (2009) describe a case of a capuchin female (*Cebus capucinus*) carrying her stillborn, arguing that she behaved in ways which suggested an awareness of her infant's death, such as letting the infant be fully submerged in water. Although this could represent causal attribution, it may equally be a failure of perspective taking. Inexperienced Japanese macaque mothers have been observed to inadvertently drown their infants when diving into the hot springs of Jigokudani Park for food (de Waal, 1996) and similar occurrences have been reported among baboons (Cheney & Seyfarth, 2007). Moreover, filial cannibalism during *post-mortem* carrying has also been witnessed, suggesting that corpses may be re-categorised as food (Altman, 1980; Hsiang-Jen & Hsiu-Hui, 2008; Dellatore, Waitt & Foitova, 2009; Watson *et al*., 2015; Tokuyama *et al*., 2017; Tian *et al*., 2016; De Marco, Cozzolino & Thierry, 2018; Watson & Matsuzawa, 2018).

Cronin *et al*. (2011) propose that whilst displaying approach–withdrawal behaviour towards the infant, the mother is actively gathering novel death cues that she could conceivably recall in equal situations (i.e. death of another conspecific). However, if the purpose of such knowledge is to prevent costly behaviours, findings from Sugiyama *et al*. (2009) that there is no significant difference in carrying duration between younger and older mothers suggests that, at least in Japanese macaques, no such learning component was found. Moreover, reports on chimpanzees from Bossou illustrate that there may be an individual component. Of the five infants that died during a flu epidemic, only two were carried for extended periods (Biro, 2011). Jire transported both her dead infants: Jokro in 1992 and again Jimato in 2003 (Matsuzawa, 1997; Biro *et al*., 2010). Similarly, in semi-ranging Japanese macaques, the same female was reported carrying her dead infant for extended periods in 2011 and again in 2013 (Watson *et al*., 2015), although other factors such as cause of death could impact these responses (see Section III.1*e*).

### (*b*) *Group–infant dynamics*

The behaviour of group members who were not emotionally involved with the infant is also of interest. Cheney & Seyfarth (2007) note that wild chacma baboons (*Papio h. ursinus*) do not attempt to handle dead infants and rarely grunt at them as they would live infants. Similarly, Rajpurohit (1997) mentions that in Hanuman langurs, other members show little interest in dead infants – a finding also reported in other species (van Lawick-Goodall, 1968; Green, 1975; Lu *et* *al*., 2007; Guo *et al*., 2016; de Marco *et al*., 2018). Conversely, infants and juveniles express more interest in the corpse (van Lawick-Goodall, 1968; Ciani, 1984; Cronin *et al*., 2011; Li *et al*., 2012), some even playing with it (van Lawick-Goodall, 1971; Hosaka *et al*., 2000; Biro, 2011). Furthermore, juvenile and nulliparous adult females have been witnessed carrying dead infants relinquished by their mothers (Warren & Williamson, 2004; Fashing *et al*., 2011). The mother occasionally restricts attempts by other group members to access the corpse (Altmann, 1980; Gupta, 2000; Li *et al*., 2012; Tokuyama *et al*., 2017) (Fig. 4), with siblings having broader admittance (van Lawick-Goodall, 1971; Kano, 1992; Muller *et al*., 1995; Matsuzawa, 1997). It is conceivable that such playful interactions may prepare younger individuals for death recognition.

The matter of stench avoidance is divisive. Byrne (2016) recounts a case in western lowland gorillas where the group members, after initial interest, seemed to avoid and shun the carrying mother after the body started to smell. Both Green (1975) and Sugiyama *et al*. (2009) report that Japanese macaque group members actively avoided the mother of a dead infant, presumably because of the putrid smell from the corpse. However, among chimpanzees (Biro *et al*., 2010) and Gelada baboons (*Theropithecus gelada*) (Fashing *et al*., 2011), no such avoidance is reported. That most mothers abandon the infant within a week of death is also informative since during this period the cadaver goes from bloating to active decay – the stage of decomposition that emanates the most stench.

Infant corpses are sometimes central to or incorporated in the displays of male chimpanzees (Bygott, 1972; Matsuzawa, 1997). Adult males have also been known to carry dead infants; most notably in semi-ranging Barbary macaques (*Macaca sylvanus*) whilst interacting with other males where the corpse is used for agonistic buffering purposes (Merz, 1978). In conjunction with other reports, Merz (1978) notes that handling was much rougher and of shorter duration than with live infants. Rare cases have involved high-ranking individuals unsuccessfully adopting live orphans and continuing to carry them after death (Taylor *et al*., 1978; Notman & Munn, 2003).

### (*c*) *Old World–New World dichotomy*

To the best of our knowledge, there are 13 published cases of dead-infant carrying among New World monkeys, comprising cebids, and atelids (see online Supporting information, Appendix S1). The lack of information on this behaviour may be partly due to the smaller number of publications on New World primates. Anderson (2011) argues that their tropical habitats accelerate the decay of corpses and consequently their abandonment. Additionally, while Old World monkeys can be either arboreal, terrestrial or both, New World monkeys are almost exclusively arboreal (Fernandez-Duque, Di Fiore & Huck, 2012). Referring to an arboreal Old World species, the red colobus (*Piliocolobus tephrosceles*), Struhsaker (2010) pointed out the difficulty of carrying a dead infant while leaping between trees – a claim supported by other colobine cases (*Colobus guereza*: Onderdonk, 2000; *Colobus vellerosus*: Teichroeb & Sicotte, 2008) and the observation that species that carry their dead for long periods, such as snub-nosed monkeys (*Rhinopithecus bieti*) tend to be more terrestrial (Long & Kirkpatrick, 1994). Observer bias may also be involved; when reviewing the literature on post-mortem carrying, the best-represented species were semi or fully terrestrial and inhabited accessible areas or were in close proximity to human communities (Sugiyama *et al*., 2009; Rajpurohit, 1997; Fashing *et al*., 2011). The only case of dead-infant carrying recorded among prosimians comes from ring-tailed lemurs (*Lemur catta*) (Nakamichi *et al*., 1996), the most terrestrial lemur (Schmidt, 2011).

### (*d*) *Non-carriers*

Not all primates engage in corpse carrying although there is evidence that they do show behavioural responses to dead or dying infants (see Appendix S2). Strepsirrhines and callithrichines generally do not carry dead infants, despite some unsuccessful attempts at carrying having been reported. Nakamichi, Koyama & Jolly (1996) observed seven cases of ring-tailed lemur behaviour towards dead/dying infants. One individual carried her dying infant tripedally for 15 m, whilst others in the troop showed affectionate behaviours, gave cohesion calls and displayed ambiguous back-and-forth movements, switching between following the troop and returning to the infant, sometimes for hours. Similarly, Santini (2012) observed a dying ring-tailed lemur infant repeatedly fall, vocalise, and attempt to climb onto the back of its mother, who wavered between staying with the infant or the group, eventually choosing the latter. Additionally, Littlefield (2010) observed two infanticides in sifakas (*Propithecus verreauxi*) where the females stayed with the dying infant, occasionally grooming it and, after its death, remaining with the corpse before giving cohesion calls and then following the group. In experimental settings with various prosimians, Rosenson (1977) noted that, whilst none of the mothers attempted to carry their dead infants, all were observed to groom them; a galago

(*Otolemur crassicaudatus*) retrieved her infant using her jaws (later and dropping it when attempting to groom), and a black lemur (*Eulemur macaco*) was seen gripping and lifting her infant. Grooming was observed in all mothers, most of which were in regular contact with their infants, likely representing an attempt to elicit a response. While it seems strepsirrhines lack the morphological proficiency for extended periods of carrying, their behaviour suggests they are not indifferent to their dead or dying infants, even after they stop showing signs of life (Nakamichi, 2016).

Callitrichines are not known to engage in dead-infant carrying, apparently relying on life cues such as movement and vocalisations to initiate carriage, consequently, care of stillborn and weak infants ceases rapidly (Rothe cited in Price, 1990). These primates have uncommon features among anthropoids as they have undergone phyletic dwarfism, possess tegulae (claw-like nails), regularly give birth to twins, and the males are the primary carriers of infants (Fernandez-Duque *et al*., 2012). Whilst there are no reports of callitrichines successfully carrying dead/dying infants, short-lived attempts can occur, with group members smelling, grooming, swatting flies, and scent-marking the infant, before ultimately abandoning it to re-join the group – an ambiguous behavioural repertoire, similar to that seen with lemurs (Digby, 1995; Roda & Pontes, 1998; Lazaro-Perea *et al*., 2000; Hilário & Ferrari, 2010; Culot *et al*., 2011). Detailed observations by Thompson *et al*. (2018) emphasise these patterns: failed attempts to carry the corpse by a male and a female, several visits to the body by group members which decreased over time, and general group interest in the corpse sustained for over 2 h with one adult male remaining in an apparent vigil after the rest of the group left (see Section III.2*c*).

The explanation for these observations may lie both in the general anatomy of these species and in their behavioural adaptations that preclude long-term dead-infant carrying (i.e. mothers do not hold newborns as the infants grab onto their fur, and unlike other anthropoids these species do not engage in bipedal carriage) (see also Rumbaugh, 1965).

### (*e*) *Contextual and sensory cues to death*

Non-human primates face death from a variety of causes ranging from predation, conspecific attack, accidental falls, disease, starvation and stillbirth. Infants may be carried *post-mortem* regardless of the cause (Fig. 5). Anderson (2011) claimed that distinct contexts of death could elicit different treatment from the living. Although it remains challenging for primatologists to record an actual moment of death, extensive records spanning decades exist for cases of infanticide (see Appendix S1 and S3). The primary mode of death in these cases is often a cranio-cervical bite (King & Steklis, 1984, 2008), leaving visible wounds to the head and spine region. Infanticide is of particular interest because (1) it affords a contextual cue (a causal chain of events leading to the death of the infant witnessed by the mother and other group members) and (2) it offers strong sensory death cues (i.e. visual cues of wounds).

Das *et al*. (2018) found that carrying duration in cases of infanticide was significantly lower in comparison to other causes of death. They attribute three subcomponents typical of human death awareness (see Table 2) to mothers carrying dead infants: repeated sensory investigation as a result of having 'Causation', handling of the inanimate infant and its defence as understanding 'Cessation', and progressive disinterest as possessing 'Irreversibility'. Their claim, however, fails to account for primate mothers exhibiting the same behaviours in other contexts. Grooming is a widespread thanatological response likely related to interest but it occurs repeatedly days after any potential causal relation was made. Defence and abandonment also occur with live infants.

Reviewing 59 cases of observed infanticides in New World and Old World primates, we found that about a third of the infants were carried by their mothers ($N = 20$) (see Tables S1.1., S1.2. and S1.4 of Appendix S1), compared to two-thirds that were not ($N = 39$) (Appendix S3). This finding supports the results of Das *et al*. (2018) and suggests that contextual and sensory death cues aid the mother's understanding of the infant's condition, allowing her to terminate her parental investment. Surprisingly, in 14 cases, infants were abandoned alive after being injured by an infanticidal male. During group takeovers, Hrdy (1974) reports that Sugiyama (1967) and Rudran (1973) interpret such cases as the mother fearing injury from the male. Nonetheless Hrdy (1974) proposed that such desertions represent a practical evaluation of the infant's condition by the mother weighing the current infant's survival chances against those of a new offspring sired by the incoming male. While she did not discuss any psychological mechanisms, it is highly likely on a proximate level that such decisions, through associative learning or higher cognitive mechanisms, are supported by contextual and physical cues of both injury and death. Other situations offering comparable sets of cues including predation (Matsuda, Tuuga & Higashi, 2008), mishandling and electrocution (Das *et al*., 2018) also lead to *post-mortem* infant desertion.

## (2) Dead group members

To some extent, interactions of living members towards dead/dying individuals indicate their prior relationship quality. There is a tendency that living group members remain for longer with dead individuals with which they had closer bonds. They may pull or hit the deceased individual, interpreted as attempts to rouse the corpse. In other situations, group members will only peer at the corpse and not come into direct contact with it (see Appendix S4). Dead-infant carrying is reported more widely than observations involving interactions with dead adults; having to forage for food, primates cannot remain in one place for long, and because adult individuals cannot be carried they are abandoned sooner. Occasionally however, dead individuals are visited days after their passing. Presumably this plays an adaptive role as visitors can monitor and update the dead individual's condition. Unlike with infants, there is considerable group involvement with adult corpses (mainly in the form of direct interactions) in multi-male/multi-female societies (Teleki, 1973; Buhl *et al*., 2012; Stewart, Piel & O'Malley, 2012; van Leeuwen *et al*., 2016; Campbell *et al*., 2016), but less so in uni-male units, particularly if the death concerns an unrelated female (Fossey, 1983; Fashing *et al*., 2011; Yang *et al*., 2016). Conceivably this relates to the social status of the individual and the social bonds it made during its lifetime, which are likely to vary depending on the individual's age, sex, kinship and rank, but also on the social organisation of that species.

A dead conspecific can cause a shift in the group's hierarchy, which translates as novel social/sexual opportunities (Anderson, 2016). The condition of the corpse may also affect these interactions with putrefied corpses eliciting fewer approaches than fresh ones (Hosaka *et al*., 2000; Hofer, Huffman & Ziesler, 2000). It has been argued that the context surrounding death might affect the reactions of other group members (Anderson, 2011; Boesch, 2012), but this remains difficult to assess given that there are so few reports of reponses to death by adult conspecifics.

### (*a*) *Direct interactions*

There are relatively few reports of responses to dead juveniles and adults, with most involving chimpanzees where responses range from peaceful to aggressive (Appendix S4). Besides peering, they may engage in gentle physical contact, such as inspecting, grooming, poking and sniffing, thus obtaining tactile and olfactory information on the state of the dead individual, and possibly attempting to elicit a response. As with dead infants (Goodall, 1977; Matsuzawa, 1997; Cronin *et al*., 2011; Biro, 2011), attention is directed towards the head or face (Box, 1984; Anderson *et al*., 2010; Buhl *et al*., 2012; van Leeuwen *et al*., 2016).

Bertrand (1969) describes interactions with corpses experimentally placed in a group of stump-tailed macaques (*Macaca arctoides*); they did not direct facial signals at them and grooming differed from social grooming (putting their feet over the face of the dead and removing chunks of fur or touching the eyes). Individuals immediately approached and touched known group members whereas unknown dead individuals were approached with caution (Bertrand, 1969).

Such contacts have been interpreted as attempts to rouse the dead or as expressions of frustration in chimpanzees (Anderson *et al*., 2010; Westoll, 2011). Galdikas (cited in Thompson, 2009) described a curious case of an orphan orangutan (*Pongo pygmaeus*) that killed two conspecifics and attempted to kill a third through drowning. On one occasion, he was observed shaking the hands of the dead orangutan as if trying to stimulate a response (for similar behaviours see Bygott, 1972; Sabater-Pi *et al*., 1993). Galdikas believed he was experimenting with life and death and seemed to appreciate the difference between these states.

Other cases seem to indicate attempts to monopolise the corpse and incorporate it in aggressive displays (Fossey, 1983; Stewart *et al*., 2012; Buhl *et al*., 2012). Copulations and mountings have been documented in these contexts directed at the corpse (Bertrand, 1969; Bezerra *et al*., 2014) and among group members (Teleki, 1973; Buhl *et al*., 2012; Pruetz *et al*., 2017). Many responses also appear to be compassionate; Bezerra *et al*. (2014) describe a wild common marmoset male exhibiting emotional/caretaking behaviours towards its dying mate such as alarm calling, embracing, sniffing and protecting the corpse. Other behaviours such as attempting to copulate as opposed to testing for a response could signify high levels of arousal.

Interactions may also include objects which are employed in different contexts. One report described a chimpanzee engaging in “corpse cleaning”, and suggested that this was both a socially meaningful way of handling the corpse and an attempt to learn about its state (van Leeuwen, Cronin & Haun, 2017; see also “investigatory probing” in McGrew, 2004, p. 124). After the death of a female lowland gorilla, King (2013) describes the male placing celery (her favourite food) on her hands. In a chimpanzee sanctuary, after a dead female was presented to her group, they groomed and attempted to tickle her, before her body was dragged and shaken by a male who, in the process, caused her face to seep blood, which was then wiped off with paper towels by another female (Westoll, 2011). Boesch (2012) detailed how leafy branches are dropped onto chimpanzee corpses, sometimes covering the bodies. He cautioned against interpreting these as "burial behaviors", since chimpanzees have been observed to do this with other dead animals, perhaps as a way to test if the body is moving. Furthermore, several monkey and ape species drop tree materials on other species, including humans, in agonistic contexts (Shumaker, Walkup & Beck, 2011). Some interactions are more violent; after the intragroup killing of a chimpanzee male, Pruetz *et al*. (2017) describe rocks being thrown at the corpse by two individuals and a third hitting it repeatedly with a stick.

### (*b*) *Guarding the body*

Guarding a corpse from perceived predators, typically expressed as mobbing behaviour, is well known in primates (reviewed in Crofoot, 2012) and avian species (Curio, 1978). The sight of a predator triggers alarm calling, harassment responses, and rescue attempts. Human and feral dog proximity to Barbary macaque  corpses has been known to provoke defence responses in conspecifics (Campbell *et al*., 2016). Gupta (2000) describes Phayre's langurs (*Trachypithecus phayrei*) forming a protective circle around a deceased female in response to vultures. Similarly, Ciani (1984) describes a rhesus macaque attacking crows that gathered around her dead infant (see also Sharma *et al*., 2011). Recently, at the Lola ya Bonobo Sanctuary, an alpha female bonobo (*Pan paniscus*) (Mimi) was recorded ferociously opposing a caretaker's removal of the corpse of a young male (Lipopo) who had died from pneumonia, despite not being close to him in life (Koerth-Baker, 2013).

Guarding the body from other group members, defined as higher-ranking individuals impeding close examination of the corpse by younger/lower-ranking individuals, is exhibited in a few primate species. Tina, a chimpanzee killed by a leopard, was observed being guarded by three adult males and a high-ranking female (who were not particularly bonded with her in life) in an interaction that lasted for six hours (Boesch, 1991). Lower ranking individuals were generally chased away, with the exception of Tina's younger brother. Bezerra *et al.* (2014), observing common marmosets, described the group's alpha male guarding the body of his dead mate while alarm calling and assuming a defensive posture, preventing juveniles and infants from approaching the corpse. Guarding the mother of a dead infant has been recorded in chimpanzees (Boesch & Boesch-Achermann, 2000) and in Gelada baboons, where a male guarded a mother with her dead infant from an infanticidal male (Mori, Iwamoto & Bekele, 1997). Occasionally among baboons, close relatives/male friends have been observed to guard an infant's body while the mother forages, and individuals will band together to defend the corpse (Cheney & Seyfarth, 2007). Guarding responses share behavioural traits with sympathetic concern and empathetic targeted helping (Pérez-Manrique & Gomila, 2018), and appear to be part of an evolved set of compassionate responses derived from neurophysiological mechanisms dedicated towards mother–infant bonding and cognitive mechanisms involved with kin-based and alliance-based based associations (reviewed in Gilbert, 2015).

### (*c*) *Vigils*

Vigils are characterised as proximity to a corpse for extended periods. Whilst also occurring in other group members, most vigils involve young orphaned primates staying near the corpse (*sensu* Fashing *et al*., 2011) (Fig. 6). Schaller (1964) gives an account of an infant mountain gorilla (*Gorilla b. beringei*) that lingered close to a silverback that had fallen ill and died (also see Vecellio, 2009). Over several days, a young Japanese macaque called and stayed in proximity to an adult female that had been killed by a raptor (Iida, 1997). An adult male howler monkey (*Alouatta palliata*) was reported to stay in the vicinity of a female's corpse for five days, interpreted as suggesting close proximity between these individuals in life (Mittermeier, 1973). Such reports are reinforced by observations where kinship and social relations are known. For example, an adult male chacma baboon (Pierre) formed a close and protective bond with an 8-month-old infant belonging to a female 'friend'. After the infant died following maternal neglect, the male stayed near the corpse for two days, hardly foraging (Cheney 1977 in Smuts, 1985). The protracted death of an elderly female chimpanzee (Ruda) in the Budongo Forest was followed by a vigil from her offspring (one infant and one juvenile) who nested beside her when night fell (Reynolds, 2005). Similar patterns are seen in captive chimpanzees; Anderson *et al*. (2010) reported that Rosie, the daughter of an elderly female Pansy, remained close to her mother's body during the night following her death. In wild chimpanzees, Stewart *et al*. (2012) reported that following the death of a female all of the males engaged in physical contact with the body, but none of the females, with the exception of the dead female's daughter, touched the body, and the daughter was the last to remain at the site after the removal of the body. The kin of a male yellow baboon (*Papio cynocephalus*) that perished from a snake bite similarly were the last to abandon the body (Strum, 1987). Thus, it appears that relationship quality, and particularly kinship, play a critical role in vigil behaviour. Vigils may be a by-product of attachment processes, conferring no evolutionary benefit; however, they could be advantageous (in the form of guarding) if the fallen individual might still recover, suggesting these animals are attempting to gather information on the dead subject's condition.

### (*d*) *Place of death: visitations and avoidance*

Visitations are defined as returns to the place where death ensued or the corpse was last seen. Such places may hold residual information about the event which can arouse curiosity or emotional distress. Smuts (1985) describes how, in the weeks following the infanticide of a yellow baboon, the bereaved mother (Zandra) became extremely agitated and called when passing the site of death, apparently initiating a search for her dead infant. In captive pottos (*Perodicticus potto*), Cowgill (1972) reported a surviving couple searching for a dead male in its usual sleeping site following its removal from the cage, and leaving portions of food, presumably for the absent male (according to the author) – a behaviour maintained even when the portion size was reduced. Following the cagemate's removal, the surviving pottos may have suffered a decrease in appetite, suggesting a grief-like response (see Section III.3*b*). Similar searches have been described in chimpanzees when no corpse was visible (van Lawick-Goodall, 1971). Perry & Manson (2009) describe capuchins, after the removal of a dead infant, alarm calling at site where the corpse was previously seen (see also Riley, Koenig & Gumers, 2015). Chimpanzees, gorillas, long-tailed macaques (*Macaca fascicularis*) and hanuman langurs have been observed returning to the place where a body was last seen and inspecting the ground (Mohnot, 1980; Prince-Hughes, 2001; Stewart *et al*., 2012; Pruetz *et al*., 2017). If the corpse is not removed, chimpanzees may revisit it the following day (Fawcett & Muhuzuma, 2000). Returning to a corpse has been recorded for wild lowland and mountain gorillas at three different sites (Robbins *et al*., 2016) and captive marmosets (Box, 1984). The chimpanzee Flint, soon after the death of his mother Flo, spent two minutes staring at a nest they had shared prior to her death. Later, he returned to the place where Flo had died and "sank deeper into depression", before his final excursion to the site, where he "curled up" and died (Goodall, 1990, p. 197). Patricia Wright (cited in Safina, 2015) reports on a family of sifakas that, after predation of the adult male, gave out lost calls and visited the corpse 14 times in five days. While some of these events may simply indicate curiosity and an attempt to obtain information on the death event, others illustrate continuation of emotional bonds after death that were maintained during life.

Avoidance of the death sites of conspecifics, has also been observed in captive chimpanzees (Anderson *et al*., 2010; E. Ichino, 2018, personal communication), although this has not yet been observed in the wild (Piel & Stewart, 2015; but see Pruetz *et al*., 2017). At the very least, this implies some comprehension that a significant event took place that carries negative emotional valence and possibly represents danger. Analogous responses have occurred in wild yellow baboons, anubis baboons (*Papio anubis*), chacma baboons and rhesus macaques where, following severe disturbance (trapping or predation events), groups abandoned their sleeping sites (reviewed in Anderson, 1984; Matsumodo-Oda, 2015). By contrast, Mohnot (1971) describes the decimation of a group of langurs in which 72 individuals died within the space of three days, possibly due to contaminated water, leaving only 11 survivors. Despite their decaying group mates being scavenged by crows and vultures and the foul odour present, surviving members continued to return to the site. It is possible that witnessing the gradual deaths of group members without any observable causation (i.e. predation) might have impacted their behaviour (for fearful responses to abrupt deaths see Teleki, 1973; Boesch, 2012).

### (3) Grieving/stress patterns

Grief is an emotional response triggered by loss and characterised by active distress and passive depression, universal in human cultures but also seen in social mammals and some birds following the loss of a parent, mate or offspring (Archer, 1999). Explanatory hypotheses include a by-product of attachment, group cohesion, a death reminder, and an honest signal of commitment (reviewed in Winegard *et al*., 2014). Whatever the proximate/ultimate causation, it is clear that grief is primarily caused by the severance of social bonds, such as the death of a significant individual, and that grieving states described in the primate literature have a substantial resemblance to human grief (Sapolsky, 2016; Anderson, 2017).

Seminal studies on mother–infant separation in macaques (Jensen & Tolman, 1962; Seay *et al*., 1962; Hinde *et al*., 1966; Kaufman & Rosenblum, 1967) did much to illustrate the emotional and behavioural responses to separation in infants. These studies described two stages: protest (categorised by marked increases in movement and vocalisation) and despair (substantial reduction in activity and intensification of self-directed behaviours). These stages were accompanied by alterations in body temperature, heart rate, endocrinal/immune system and neurochemistry, together with decreases in food and water intake, and in some cases were followed by death (Spencer-Booth & Hinde, 1971; Gilmer & McKinney, 2003).

### (*a*) *Orphans*

A few observations have detailed how infant and juvenile primates respond to the death of their mother. Mohnot (1980) describes a 28-week-old langur vocalising in visible acute and prolonged agitation whilst in physical contact with the corpse. Fashing *et al*. (2011) describe an orphan gelada (Tussock) vocalising and rocking beside her dead mother away from the rest of the group; she died the following day. Goodall (1986) outlined the behavioural changes of nine orphaned chimpanzees, including lethargy, decreased play, loss of appetite, and emaciation. The most severe case was of Flint who was considerably attached to his mother and, after her death, fell into a depressive state, that ended in his death three weeks later (Goodall, 1990). Goodall (1990) also recounts the case of the juvenile Pax who became agitated and screamed following his mother's (Passion) death, constantly pulling her hand and carrying out a vigil with his two elder siblings, moving away before nightfall. Successful adoptions have a positive effect, as seen in a captive orangutan that spent more time in physical contact with her aunt after her mother died and showed no significant self-directed behaviours (Whilde & Marples, 2011).

### (*b*) *Group companions*

The loss of an infant may trigger a grief response in the mother. De Waal (1996) vividly illustrates the case of a captive chimpanzee that whimpered and wailed after the loss of her infant (see also Blair, 1920). The wild chimpanzee Pom, after the death of her infant from an accidental fall, became lethargic and emaciated to a life-threatening point, eventually readjusting by developing a closer relationship with her own mother (Goodall, 1990). In chacma baboons, recording a total of 26 deaths, Engh *et al*. (2006) reported that stress levels were particularly high for females who had lost a relative when compared to control females. These "bereaved" females seemed to compensate by widening and reinforcing their grooming network, which the authors suggest would have returned their stress levels to baseline. Additional research on these baboons found temperamental differences impacting the success of friendship formation after the death of a relative (Seyfarth & Cheney, 2013). Likewise, Kaplan *et al*. (2012) recorded a more than doubling in stress levels in a group of common marmosets following the accidental death of a roommate; stress levels remained high for 3 days. Despite not observing overt signs of grief, Fossey (1983) reported similar readjustments (playing with juveniles) in primiparous female mountain gorillas whose infants were subject to infanticide, perhaps, the author suggests, strengthening social ties. In captive lowland gorillas, after the loss of the dominant male (silverback), both mother–infant bonds and female–female aggression intensified (Hoff, Holt & Marple, 1998). Self-directed and other behaviours indicative of stress also increased in two captive gorilla populations (Less *et al*., 2010). In captive siamangs (*Symphalangus syndactylus*), Orgeldinger (1996) reported significant behavioural changes in the male and female of a pair following the death of their infant, with increased levels of play, bonding, and sexual and agonistic behaviours and decreased territorial behaviours. Majolo & McFarland (2009) report self-suckling in wild Barbary macaques after the loss of their infants, suggesting that it may have a stress-releasing function.

Social withdrawal in primates can also be construed as an expression of grief. Reports on snub-nosed monkeys describe females ceasing social activities during and in the first days after the death of their infants (Li *et al*., 2012; Guo *et al*., 2016). According to Green (1975), macaque mothers of dead infants exhibit low activity levels, a sagging posture, an overall depressive appearance, and social withdrawal – although it is difficult to ascertain whether the latter is an active choice by the mother or the result of others moving away from her dead infant. In captive great apes, in response to the loss of an established member the whole group experiences appetite reduction and decreased activity (de Waal, 1996, 2013; Anderson *et al*., 2010; Less *et al*., 2010) A similar pattern is seen in wild snub-nosed monkeys (Guo *et al*., 2016). Several accounts describe how a chimpanzee group can become silent following a death, whether caused by fatal aggression (de Waal, 1986; Pruetz *et al*., 2017), disease (de Waal, 1996, 2013), or old age (Anderson *et al*., 2010).

### (*c*) *Grief and awareness*

Grief by itself does not presuppose an awareness of death. Despite many thanatological reports, primates have seldom been witnessed comforting grieving group members (Cheney & Seyfarth, 1990, 2007). Box (1984) reports the death of a captive female common marmoset in which the male spent time grooming her and scent marking. After the body was removed the eldest daughter groomed her father attentively in addition to scent marking. In her behaviour she seemed to be assuming the role of her dead mother. While the male protested at the removal of the corpse, within minutes, he and the whole group became calm. An account describing how a young Japanese macaque female clutching her dead infant and wailing was embraced by her own mother illustrates the difficulty of interpreting such events as consoling (Green *in* Pierotti & Annett, 2014). Yoshida (1994) describes a captive group of chimpanzees staying in close proximity to a bereaved mother for longer durations than usual and grooming her. Mohnot (1980) also reports three adult hanuman langur females intercepting an agitated orphan, embracing him and preventing him from approaching his dead mother.

Naturally, single observations such as these do not allow us to ascribe motivation to the consoler concerning the griever's state. The most parsimonious explanation in some if not all cases is that the consolers simply respond to the subject's emotional state, regardless of any causal attribution to their condition. Empathy does not operate solely on cognitive levels, at its basis being a spontaneous emotional contagion response (see de Waal, 2008).

### (4) Interactions with dead non-conspecifics

Primates share their habitats with other species. Thus, it is of interest to consider whether there are differences between their responses to a corpse of their own species compared to another species. Do their responses fall on an animacy continuum, where phylogenetically close groups elicit more similar responses than those for phylogenetically distant groups? Preliminary data suggest that adult-sized and infant-sized mammal non-conspecifics elicit similar responses in primates to adult and infant conspecifics, respectively. In wild yellow baboons, Hausfater (1976) observed a nulliparous female carrying a dead rat clutched to her ventrum until it was snatched by two juveniles who licked it, and another female who attempted to groom it (see also Loveridge, 1921). In wild chimpanzees, analogous responses were seen in a young female towards dead rodents (van Lawick-Goodall, 1968), and similar behaviours have been reported in females carrying a limb of a dead colobus (*Procolobus rufomitratus*) and dead hyraxes

(*Dendrohyrax dorsalis*) (Hirata *et al*., 2001; Cibot, Sabiiti & McLennan, 2017). Another case included an old female bonobo carrying a dead red-tailed monkey (*Cercopithecus ascani*) for 43 days (Toda, Tokuyama & Furuichi, 2017). Additionally, in Barbary macaques, males have been observed using dead rabbits in triadic male interactions in place of infants (Turckheim & Mertz, 1984).

Some cases refer to 'animal toying' in great apes (Boesch & Boesch, 1989; Zamma, 2002; Hirata & Mizuno, 2011;), in which an individual will seize a heterospecific and interact with it in a playful manner, sometimes killing it in the process. A leopard cub (*Panthera pardus*) that was killed by adult chimpanzee males, was then carried like an infant for hours by a young female (Hiraiwa-Hasegawa *et al*., 1986). In wild bonobos, two cases were observed where young males carried and interacted with live infant red-tailed monkeys which died, likely due to rough handling. Following their death, the bonobos attempted to make the monkeys take hold of them and one bonobo raised the monkeys' arms and let them fall numerous times (Sabater-Pi *et al*., 1993).

While chimpanzees hunt a variety of animals, they only rarely scavenge on fresh carcasses or feed on animals not killed in their presence by other chimpanzees (Watts, 2008; Newton-Fisher, 2015). In fact, chimpanzees sometimes show apprehensive or fearful responses towards dead heterospecifics (Goodall, 1986; Nishida, 1994). Muller *et al*. (1995) described Gombe chimpanzees interacting with a dead adult bushbuck (*Tragelaphus scriptus*) – swatting flies, poking, grooming, sniffing, 'huu' calling, etc. – noting that only small pieces of flesh were consumed, and solely by juveniles, with similar episodes witnessed at Ngogo (Watts, 2008). Comparable responses have been observed to corpses of aardvarks (*Orycteropus afer*) (Hosaka, Inoue & Fujimoto, 2014) and bushpigs (*Potamochoerus larvatus*) or leopards (Nishida, 2012). The classic field experiments of Kortlandt (1967) in wild chimpanzees revealed that they were more fearful of dead and seemingly dead mammals or mammal models (mangabey, goat, antelope) then when these were presented in lifelike postures. By contrast live animals were met with little fear. In anubis baboons, experiments conducted at the Gilgil site, Kenya, show a behavioural pattern possibly widespread among primates. When presented with gazelle carcasses, baboons that had eaten from the carcass previously or observed others do so were more likely to feed from it, whilst individuals with no prior contact with the carcass rejected it (Strum, 1983).

These observations suggest some resemblance between responses towards conspecifics and non-conspecifics. This may be because corpses are not seen as potential prey (Boesch & Boesch, 1989), generate an unusual/unfamiliar feeling that promotes fear or curiosity (Hosaka *et al*., 2014), or that a pathogen avoidance mechanism is involved (Watts, 2008) which would explain why scavenging observations are rare. There is little/no consumption by chimpanzees of corpses caught by leopards, a predator of chimpanzees (Muller *et al*., 1995; Watts, 2008; Nishida, 2012; Hosaka *et al*., 2014), with recorded cases either representing assumptions or confounded by human interaction (Hasegawa *et al*., 1983).

## IV. PRIMATE THANATOLOGY: EVOLUTIONARY/COGNITIVE ASPECTS

### (1) A naïve theory of life

Primates divide their world into agents and non-agents. Agents are living entities capable of engaging in self-generated motion, exhibiting goal-directedness and contingency, and acting upon and reacting to objects, events and other agents in their world (Barrett, 2005; Spelke & Kinzler, 2007; Carey, 2009). This conserved perceptual-cognitive feature conveys a critical advantage in predator–prey detection. In a visual world, many animals have evolved ways to conceal themselves *via* mimicry or colour change (Stevens & Merilaita, 2009), or engage in behaviours such as freezing (Hagenaars, Oitzl, & Roelofs, 2014) or thanatosis (Humphreys & Ruxton, 2018).

In primates, life detection is one of many Core Knowledge Systems, in this case, the Core System of Agency (CSA), for which there is evidence for a dedicated neural pathway in macaques (Sliwa & Freiwald, 2017). Core Knowledge Theory proposes that hard-wired cognitive skills shape mental representations about the world (Carey, 2009). Using Leslie's (1994) tripartite division of agency as a starting point, we outline how life is perceived in primate brains at three levels of agency:

(1) *Animate agency* – this level pertains to the animacy detection system and is governed by two dimensions: shape and movement. These perceptual cues arise in the form of mechanisms such as biological motion perception, a gaze detection module, and a face detection module, comprising components partly of innate character and partly acquired during ontogeny.

Detecting eyes looking directly at the observer conveys information critical for survival; computations such as this in predator–prey interactions have been termed 'the beginnings of mind-reading' (Barrett, 2015). The existence of an eye-direction detector (EDD) or gaze detection module was proposed by Baron-Cohen (1995) as a specialised neural system that functions by sensing eyes and eye-like stimuli in the environment. In the primate social sphere, attending to eyes can arbitrate both affiliative and aggressive interactions (Emery, 2000), and its effectiveness as a stimulus has been shown in the cognition literature (Batki *et al*., 2000; Myowa-Yamakoshi & Tomonaga, 2001; Myowa-Yamakoshi *et al*., 2003; Farroni, Johnson & Csibra, 2004). From birth, primates engage in face-to-face exchanges.

Biological motion perception has been interpreted as a perceptual life detector common to vertebrates and understood as a tendency to attend to the semi-rigid movements typically exhibited by animals (Johnson, 2006; Troje & Westhoff, 2006; Vallortigara & Regolin, 2006). Comparable results have been found in several species, including primates (reviewed in Gonçalves & Biro, 2018). In rhesus macaques, this information is processed in the superior temporal sulcus (STS) which shows homology to humans (Jastorff *et al*., 2012). Additionally, a face-detection module appears to exist that is dedicated to processing, at the subcortical level, faces in the environment (Morton & Johnson, 1991; Johnson, 2005).

(2) *Intentional agency* – built upon animate agency, intentional agency is governed by behaviour reading. This implies a reasoning involving little mental state attribution, focusing instead on behavioural regularities and contextual signals. It is grounded on goal-attribution mechanisms such as gaze following and joint attention and is triggered by cues such as eye orientation, head position and body posture.

Several primate species show sensitivity to human goal-directed action, including apes (Call *et al*., 2004; Uller, 2004), Old World monkeys (Rochat *et al*., 2008), and New World monkeys (Phillips *et al*., 2009; Santos & Hauser, 1999; Burkart *et al*., 2012). Previous experience plays a role in shaping the predictions of the observing animal (Rochat *et al*., 2008; Burkart *et al*., 2012; Simpson *et al*., 2016). Intentions are also scrutinised through behavioural actions (Call *et al*., 2004; Phillips *et al*., 2009, Canteloup & Meunier, 2017) and gaze following, which facilitates joint attention orienting towards objects or events and undergoes predictable ontogenic shifts (Rosati *et al*., 2016).

For perspective taking, there seems to be a difference between Old and New World primates. In hidden food experiments, using the conspecific competition paradigm, capuchin monkeys (Hare *et al*., 2003) and common marmosets (Burkart & Heschl, 2007), unlike chimpanzees (Hare *et al*., 2000; Hare, Call & Tomasello, 2001) and rhesus macaques (Flombaum & Santos, 2005), consistently fail to reason about what the competitor can and cannot see. Such abilities appear to require a more mentalistic kind of agency.

(3) *Mentalistic agency* – researchers have long endeavoured to uncover a theory of mind (inferring the mental states of others) in non-human animals (reviewed in Call & Tomasello, 2008). Monkeys appear unable to do this (Martin & Santos, 2014), with sensitivity to the existence of rivals and their gaze path as simpler explanations than connecting the act of seeing to knowing (MacLean & Hare, 2012). One suggested mental device that uses mind-reading abilities is experience projection, which has been demonstrated in chimpanzees (Karg *et al*., 2015). It was proposed that chimpanzees might possess a minimal theory of mind with false-belief attribution being a limiting boundary of their mindreading capabilities (Call & Tomasello, 2008); however, recent studies (Krupeneye *et al*., 2016; Buttelmann *et al*., 2017) have revealed that great apes do possess implicit knowledge of false-beliefs – a fundamental aspect of the theory of mind.

## (2) Levels of death awareness

Despite the abundance of multimodal cues that could potentially inform primates of death when they encounter it in novel situations (Fig. 7), it remains unclear whether they are ‘cognitively blind’ to such information or if they possess an understanding of the phenomenon of death.

The CSA functions to detect live entities, guaranteeing effective interaction with the animate world. This is best illustrated by contrasting the costs and benefits associated with predator-detection accuracy: successfully discriminating a live predator from a dead one allows the activation of different decision-making actions with clear advantages for survival and reproduction, whilst failure may result in death (Barrett, 2005). It is unclear whether a death-detection mechanism exists, either in parallel to the agency system, or as part of a generalised threat detection mechanism. How would a concept such as ‘ex-agent’ emerge? We propose a three-level division of death cognisance which relates both to the cognitive/developmental and phylogenetic levels of the primate order.

(1) *Animate/inanimate distinction* – in humans, both animate and inanimate conceptual categories appear to be employed by distinct neural circuits representing domain-specific,

evolutionarily adapted knowledge systems (Caramazza & Shelton, 1998; Naselaris, Stansbury & Gallant, 2012) – a claim supported by primate brain research on the inferior temporal cortex of rhesus macaques (Kiani *et al*., 2007; Kriegeskorte *et al*., 2008; Bell *et al*., 2009). The animate/inanimate distinction level likely operates through dual Core Knowledge Systems specialised for dealing with animate and inanimate entities, the CSA and the Core System of Object (CSO), respectively. Objects, contrary to agents, are predictable and inert, moving only when external force is applied.

We know that monkeys recognise that a solid object cannot pass through another solid object (Santos & Hauser, 2002) or move unless contacted by another moving object (Hauser, 1998). When seeing a human reaching for an object, five and seven-month-old infants react to changes in their goals (Woodward, 1998); no such response is observed when a rod/claw reaches for the same object (Woodward, Somemerville & Guajardo, 2001; Hofer, Hauf & Aschersteben, 2005; Daum & Gredebäck, 2011) unless replaced by a realistic humanoid robot (Kamewari *et al*., 2005; also see Arita *et al*., 2005). Similar results have been found in capuchin monkeys (*Sapajus apella*) (Phillips *et al*., 2009), whilst in common marmosets the use of a monkey-like robot, but not a moving box, induces goal-direction ascription (Kupferberg, Glasauer & Burkart, 2013). While human infants (of nine, 10 and 18 months) tend to imitate the goal-directedness of a human actor, they do not readily imitate analogous actions of a mechanical actor (Meltzoff, 1995; Legerstee & Markova, 2008, Boyer, Pan & Bertenthal, 2011). Infants (of 12 weeks and two months) show differences in looking time when presented with a human *versus* a toy monkey, and smile and coo only with the former (Brazelton, Koslowski & Main, 1974; Trevarthen, 1977). Seven-month-olds appreciate that humans, but not objects, can exhibit self-propelled motion (Spelke, Phillips & Woodward, 1995; Markson & Spelke 2006), and nine-month-olds become distressed upon seeing inanimates moving on their own (Poulin-Dubois, Lepage & Ferland, 1996). Even to the naïve brain, movement by itself is not a sufficient condition for agency – a rule that makes sense for all species, since, while the natural world can produce animate movement in inanimates, it does so in a predictable fashion (i.e. rivers, falling leaves, rain). Only upon encountering agents or entities with agent-like properties is the CSA activated.

(2) *Living/non-living discrimination* – the death of a group member represents an ecological scenario of expectancy violation as implied by the surprise, fear and puzzlement

group members exhibit towards the dead. At a cognitive level, the corpse activates the CSA by virtue of its static cues to animacy, but because its affordances are that of an object, it also triggers the CSO. This perceptual mismatch creates a conflict in the two core systems, causing an *animacy detection malfunction* (Gonçalves & Biro, 2018). When a familiar individual is displayed in an unfamiliar configuration it triggers a complex chain of survival-critical reactions, chiefly processed by the limbic system, which direct attention to potential danger. Comparative neuroimaging studies show that both the hippocampus and the amygdala are activated during states of uncertainty, and are part of a neural novelty detection circuit (Blackford *et al*., 2010; Balderston, Schultz & Helmstetter, 2013; Maren, 2014). Research shows that the hippocampus is a mismatch detector *par excellence* (Kumaran & Maguire, 2007), while the amygdala plays a part in detecting biologically relevant stimuli and threat assessment (Whalen, 2007). When these regions are damaged, as shown by primate brain lesion research, subjects exhibit diminished fear and vigilance to threat (reviewed in Rosen & Donley, 2006).

These brain areas are also critical for learning processes. Clearly, death is a common occurrence in the animal kingdom. It has been claimed that primates might be able to distinguish between the presence and absence of agency (Anderson, 2011), making it conceivable that group members that have witnessed such events before can gather both contextual and sensory information to be retrieved on similar occasions (Gonçalves & Biro, 2018). Notably, since primates live in social environments, there are abundant opportunities for them to interact with dead conspecifics, acquaint themselves with death cues and integrate them in a limited sense (i.e. a dead individual that once afforded movement and sound is gradually re-categorised as one that does neither). Observations on monkeys suggest that this re-categorisation is rather fluid. Booth (1962) notes that captive vervet monkeys (*Chlorocebus aethiops*) sometimes abandon sickly infants too weak to move and appearing dead. Moreover, she observed that if stillborns are accidentally pushed by the mother resulting in short-term movement or if a human observer deliberately pushes it making it appear to be self-propelled, the mother's attention is instantly activated, stimulating her to lick it in an agitated fashion. Correspondingly, and contrary to a non-responsive infant, a moving stuffed natal coat carried by a human triggers rescue attempts from the group, which subside as soon as the infant skin is left motionless (see also *post-mortem* spasms; Anderson *et al*., 2010; Pruetz *et al*., 2017).

Finally, since the corpse of a conspecific may evidence a predation event and consequently critical danger, natural selection might have acted on developmental systems that promote rapid acquisition of such knowledge through associative learning mechanisms *via* social knowledge – basic phenomena shared by many animals but separate from notions of death as a universal and permanent state.

(3) *Death awareness* – dead is not the same thing as death (Kastenbaum, 2000): dead (the state) is the physical result of the phenomenon of death (the event). Awareness of death has been a considerable object of study in developmental psychology (Speece & Brent, 1996; Slaughter, Jaakkola & Carey, 1999; Kenyon, 2001). Research on the concept of death in humans, generally in the form of structured interviews, suggests that children acquire separate subcomponents of death at distinct periods in development (see Table 2).

Many factors are involved in the acquisition of a mature concept of death such as age, cognitive development, and previous experience (Hunter & Smith, 2008). Evidence shows that children grasp the physical aspects of Cessation (body stops functioning) and understand its psychological aspects (dead cannot think nor dream) (Bering, McLeod & Shakelford, 2005). Likewise for Causation, younger children realise that external factors (accidents, predation, etc.), cause death before they comprehend that internal factors (breakdown of bodily functions) contribute to it. Without this 'scientific' aspect of Causation (Kenyon, 2001) a mature concept of death would be acquired at earlier ages. Experience with death appears to accelerate death-concept acquisition; children with direct death experience show a more mature understanding of death *versus* inexperienced age-mates (Kenyon, 2001; Hunter & Smith 2008; Bonoti, Leondari & Mastora, 2013). Same-age groups tend to show similar understanding regarding animal death, again likely due to previous experience (Orbach *et al*., 1987; Bonoti *et al*., 2013). Studies using realistic stimuli (photographs or stuffed animals) found that three year olds performed significantly better in discriminating living *versus* dead states than conventional studies (i.e. interviews) show [Behrend (1984) and Sprent *et al*. (1996) both cited in Barrett & Behne, 2005]. Indeed, exposure to corpses remains a powerful source of knowledge of death for young children (Astuti, 2011). As they attain a concept of death, children seemingly rely on inductive and analogical reasoning to achieve and revise it by extending human qualities/experiences to other scenarios including living beings (Carey, 1985; Slaughter, 2005).

One standout study is that of Barrett & Behne (2005). Contradicting previous claims, they argued for a death detection mechanism, which functions as a subroutine of the CSA (or agency detection system) that switches off agency inferences when reliable cues to death are available. To test their cessation of agency hypothesis, they interviewed two populations of children from different cultural backgrounds on sleep *versus* death conditions, and found that children as young as four already show a clear understanding of death with regards to Causation and Cessation, suggesting a strong mechanism regardless of personal and cultural differences (Barrett & Behne, 2005; Barrett, 2005).

Their cessation of agency hypothesis (Barrett & Behne, 2005; Barrett, 2005) makes a few important claims about death inferences in an evolutionary framework. In ancestral environments, members of the *Homo* lineage would have encountered a variety of living animals which they were already naturally selected to monitor as possible sources of danger (see Section III.1). Through frequent interaction with dead animals, including potential sources of food, reliable cues to and/or knowledge of the cause of death would activate a 'switch' or an expectancy shift (Kastenbaum, 2000) promoting a re-categorisation from living to dead. Not being able to make such a distinction would be energetically costly since it unnecessarily prolongs alert states (Dukas & Clark, 1995).

At Täi Forest, Boesch (2012) observed chimpanzees displaying more fearful reactions to dead individuals that died of disease than to individuals that died from leopard predation (10 cases *versus* 5 cases, respectively). Moreover, they tended to lick wounds of injured conspecifics, something they never did with dead ones. These distinctions seemed to rely on an understanding of death when reliable cues were available and appear to indicate chimpanzees have an implicit awareness of death; living individuals have their wounds tended, dead ones do not, and unexplainable deaths (no visible wounds) rather than explainable ones (visible wounds) induce the most fear. Taken together these reports imply that chimpanzees may have a limited capacity for the subcomponents of Causality and Irreversibility.

Irreversibility can also be assessed through violation of expectations: when a dead individual is confidently re-categorised as dead, seeing it alive again can elicit a strong emotional response. An anecdote by de Waal (2001) illustrates such a scenario in captive chimpanzees. In the Arnhem Zoo, a documentary had been produced depicting its chimpanzee population. During its development one male Nikkie, had died. When the documentary was projected to them and when the dead chimpanzee appeared on screen the two remaining males had a fearful reaction: “It remains unclear whether the apes recognized the actors, until a life-sized Nikkie appeared. At that point Dandy immediately ran screaming to Yeroen, jumping literally in the old male’s lap! Yeroen, too, had an uncertain grin on his face. Nikkie’s mysterious resurrection had temporarily restored their old pact.” (de Waal, 2001, p. 305).

Kordlandt (1967, p. 204) observed fearful responses in wild chimpanzees to experimentally placed dead or dead-like mammals in contrast to living ones, and concluded that “chimpanzees have some kind of notion what life and death are, (…) however vague this notion might be”. Bering (2001) argued that chimpanzees possess an awareness of biological death, meaning, like three-year-old humans, that they appreciate changes in state, but do not possess an awareness of psychological death (the end of cognitive functions). Other researchers have made bolder claims. Gallup (1979, 1998), through his mirror self-recognition experiments on great apes, suggested that with self-awareness comes an awareness of one’s own mortality. Premack (1976) raised the possibility of teaching a chimpanzee about its own future death, but dismissed it on ethical grounds, while ASL studies on great apes remain inconclusive (Patterson & Gordon, 1993; Fouts & Mills 1997). Likewise, de Waal, stated that “Seeing the termination of a familiar individual’s life, chimpanzees may respond emotionally as if realising, however vaguely, what death means” (de Waal, 1996, p. 56), and that “might these individuals not apply what they have learned about life and death to their own bodies? It’s hard to know, yet impossible to rule out.” (de Waal, 2013, p. 210). Such ability would likely require a capacity for the animal to mentally project itself into the future, and there is convincing evidence that great apes can do this in other contexts (reviewed in Osvath, 2016).

The rather persuasive examples of non-human primate awareness of death mainly include the great apes. In comparison to monkeys, great apes perform better at cognitive tasks requiring the use of analogical reasoning, future-oriented reasoning and mirror self-recognition, with monkeys usually needing extensive training to succeed at such tasks (reviewed in Vonk, 2003; Osvath & Persson, 2013; Anderson & Gallup, 2015; Thompson, Flemming & Hagmann, 2016). Taken together, they suggest that these cognitive abilities are not as normative in monkeys as they appear to be in great apes. Many of these abilities are related to executive functions, high-level cognitive processes that optimise behaviour, believed to emerge mainly in the prefrontal cortex (i.e. emotional regulation, inhibitory control, working memory and forethought). The prefrontal cortex underwent considerable expansion during ape evolution – a trend beginning in the Miocene 19–15 million years ago (mya) and continued in the genus *Homo* (Smaers *et al*., 2017). As a whole, these studies along with captive and wild thanatological reports place great apes as the likeliest candidates for achieving aspects of a human-like concept of death (i.e. irreversibility, causation), nonetheless the burden of proof still awaits future research.

In conclusion, primates and other socially complex animals, *via* their sensory modalities and cognitive and learning processes, can distinguish dead from live states (Gonçalves & Biro, 2018) (Fig. 8). However, the claim that primates may have more than an implicit awareness of death currently stands on *terra incognita*; the available evidence, while highly suggestive, is not yet the most compelling.

### (3) Grief becomes mourning

Conjectures have been made regarding the thanatological behaviour of extinct primates. Pettitt (2011), assessing data from chimpanzees, suggested that such behaviours might reach as far back as the Miocene apes 23–5 mya. Given that the fossil record for anthropoids emerges some 45 mya (Beard, 2016), and that dead-infant carrying is prevalent among extant monkeys and apes, it is likely that this practice was present throughout the Eocene and well into the Pleistocene, with all the behavioural features that accompany it. The living primate species that engage most often in dead-infant carrying behaviour are typically terrestrial and/or capable of bipedal carriage, implying that hominin lineages with brain capacities and structure comparable to chimpanzees, such as ardipithecines and australopithecines (Suwa *et al*., 2009), may have carried their dead infants and exhibited a similar thanatological repertoire to extant great apes.

During human evolution, such behaviours gradually gave way to more ritualised mortuary activities, including burial practices and beliefs in the afterlife (Stiner, 2017). This transition has not been thoroughly placed in an evolutionary framework, with three noteworthy exceptions from the fields of archaeology (Pettitt, 2011), philosophy (Sheets-Johnstone, 1986), and primatology (Anderson, 2017). Pettitt (2011) outlined five stages of mortuary behaviour development: core mortuary, archaic mortuary, modernising mortuary, modern mortuary, and advanced mortuary. The behaviours described herein constitute the core mortuary phase, present in apes and anthropoid monkeys, with the corpse invariably being relinquished *in situ*. The later stages of mortuary behaviour are characterised by the mode in which the corpse is left; structured abandonment (deliberate deposition of the corpse in a given place) and funerary caching (placement of the corpse in pits, caves or natural fissures) occur in the archaic mortuary phase, whilst cairn covering (stones covering the corpse) and inhumation occur as part of the modernising mortuary phase. Boesch (2012) observed chimpanzee corpses at Täi forest being covered with leafy branches by conspecifics. However, similar to the evolution of nest building in great apes (Sept, 1998), it remains challenging to determine whether comparable behaviours occurred in hominins due to the perishable nature of such materials. Nonetheless, this could account for the large gaps in the morturary record during the archaic mortuary phase.

Despite being matters of contention, there are archaeological sites that may fill the mortuary gaps in the Palaeolithic period. Pettitt (2011) interprets the AL-333 fossil site as an example of structured abandonment, containing the corpses of some 13 individuals of *Australopithecus afarensis* that were presumably placed in a field amidst tall grass by their conspecifics around 3–3.5 mya. The earliest probable examples of funerary caching were practiced by *Homo heidelbergensis* around 350–450 thousand years ago (kya) (Carbonell & Mosquera, 2006; Sala *et al*., 2016) and *Homo naledi* at 236–335 kya (Dirks *et al*., 2015; Berger *et al*., 2017), with *Homo neanderthalensis* and *Homo sapiens* burials overlapping from 80–34 kya (Pettitt, 2015).

What do mortuary and funerary rituals signal and what purpose do they serve? In the case of Palaeolithic burials, the underlying motivations appear to be of compassionate nature rather than practical disposal. An observable trait of earlier hominins is their high degree of compassion, where group members took care of their sick and injured, delaying their demise (reviewed in Hublin, 2009). Stiner (2017) makes important claims regarding this. First, most of these burials occur in residential campsites within or near social sites significant to the living. Second, since the assortment of animal carcasses and organic remains often found scattered in camps would have contributed to strong smells, burying a group member to remove the offensive stench seems unlikely. Third, considering these were nomadic groups, moving camp rather than cleaning up and leaving the bodies along with other animal remains would have required less effort. Finally, rather than burying a corpse so as not to attract potential scavengers (Boyer, 2001) our ancestors might have been simply displaying care for the deceased by protecting them from scavengers.

Rossano (2015) argues that the elaborate burials seen in the Upper Paleolithic have a ritualistic component indicating behavioural cost in terms of time, effort and resources, all of which evidence credible displays of social commitment. However, short of relinquishing the corpse *in situ*, any mortuary treatment will involve a cost regardless of ritual components. Deliberate placing of corpses in a specific open areas (structured abandonment) or natural fissures or caves (funerary caching) involves moving them to such places. They must have been carried/dragged by either one individual which is energetically demanding and suggests close emotional bonds or, perhaps, as a group effort which, albeit less demanding, undeniably indicates shared intentionality. Shared intentionality (i.e. the ability to share attention and emotional/cognitive states and coordinate actions grounded in these states) is described as a foundational human behavioural feature (Tomasello & Carpenter, 2007). At a basic level, these practices show that earlier hominins appreciated that death was a different state and thus corpses required particular treatment.

Noting the extensive exposure to death cues through visual and physical contact directed at corpses across human cultures, White, Marin & Fessler (2017) propose that mourning rituals serve an evolutionarily selected purpose. The death of a group member may not only be detrimental to immediate family by decreasing inclusive fitness but would also impact the wider group. Functionally speaking, mourning ceremonies shorten the grieving process by allowing ritualised re-categorisation from living to dead and facilitate the restructuring of social bonds through replacement. Moreover, in modern humans, mothers that hold their dead stillborn report fewer anxiety and depressive symptoms in comparison to mothers that do not (Cacciatore, Rådestad & Frøen, 2008) suggesting a grief-management component to such practices.

Extant primates, due to ecological and evolutionary constraints (i.e. foraging lifestyle), typically abandon injured/sick individuals. That is not to say they show no empathy or concern in the contexts of death, injury and disease (see Boesch *et al*, 2010, Pruetz, 2011; Tokuyama *et al.*, 2012; Bezerra *et al.*, 2014), rather their treatment of such individuals is mostly confined to the mother–infant bond (Turner, Gould & Duffus, 2005; Matsumoto *et al.*, 2016). Abandonment of ill/fatally injured individuals is the culmination of what is often a protracted surrender of such individuals by their group (van Lawick-Goodall, 1971; Fossey, 1983; Goodall, 1986; Strum, 1987; Yang *et al.*, 2016). However, their failure to engage in the more elaborate mortuary behaviours exhibited by early hominins indicates a cognitive disparity between human and non-human primates. Since the panini (chimpanzees and bonobos) and hominini lineages diverged some 5–7 mya, the latter underwent significant physical and behavioural innovations. Biological trends included bipedal specialisations and increased brain size (from the 400 cm$^3$ of Australopithecines to the roughly 1400 cm$^3$ of *Homo sapiens*) but also cortical re-organisation (increased dominance of the prefrontal regions) (Holloway, 2015). Behavioural advances included a flaked stone industry with increased technological complexity over time (Toth & Schick, 2018), emergence of language (Morgan *et al*., 2015), control of fire as early as 1mya (Berna *et al*., 2012) and the appearance of the funeral rituals discussed above. Together, these examples illustrate a growth in intellect and prosociality in our lineage with levels far exceeding those observed in primates today.

## (4) General findings and future directions

Historical records of thanatological responses in primates span over two centuries, well before ethology and primatology were established fields. Due to its prevalence across primate taxa, particularly anthropoids, dead-infant carrying along with other thanatological interactions likely took place as early as 45 mya. With regards to the cognitive mechanisms underlying such behaviours it is most parsimonious that dead-infant carrying, guarding, vigils and visitations reflect a limited awareness of death (i.e. the individual ceased agency) that requires constant status updating. From an evolutionary perspective, caregiving activities directed at temporarily inactive individuals would be advantageous if inanimate individuals could recover, consequently primate mothers and other individuals with close bonds to the deceased are expected to display such behaviours. In such cases, emotional motivations underlying these behaviours may temporarily override the more cognitive aspects of death recognition. This is evidenced by the behaviour of other individuals, less strongly bonded with the dead, who cease their interactions sooner. Previous experience of death, especially when both contextual and perceptual cues to death are available (through mechanisms such as associative learning and/or causal reasoning), appears to accelerate abandonment and diminish carrying durations of infant victims of violent deaths (i.e. predation, infanticide).

Loss of a social partner can negatively impact fitness in the living and promote a shift in the hierarchical order. Assuming that primates can extract valuable albeit limited information from dead conspecifics (*sensu* Cronin *et al*., 2011; White *et al*., 2017), there are indirect evolutionary benefits to thanatological responses. In the context of a social group, we suggest interactions with the dead: (1) promote more rapid re-categorisation from living to dead; (2) decrease costly vigilance/caregiving behaviours; (3) are crucial to the management of grieving responses; (4) update individual position in the group hierarchy; and (5) accelerate the formation of new social bonds.

Acquisition of an advanced concept of death (with the subcomponents of Universality, Irreversibility, Cessation and Causation) developed during human evolution through the expansion of the neocortex. This allowed abilities to develop such as high-order reasoning, essential to an understanding of death as suggested by archaeological evidence on mortuary practices among our ancestors in the genus *Homo* and the developmental/cognitive literature in humans.

Primate thanatology has recently benefitted from careful ethological observations which could be complemented by hormonal measurements (Engh *et al*., 2006; Kaplan *et al*., 2012) carried out in a systematic fashion. Social Network Analysis could provide a useful tool to analyse the social impact on a group of the death of one of its members (*sensu* Kanngiesser *et al*., 2011). Relating to the claim that wild chimpanzees do not tend to wounds of the dead (Boesch, 2012), we do not know if this also applies to other less cognitively complex primate species known to tend wounds in the living. We also know very little about the occurrence of visitations to a corpse, since primate groups can be difficult to track; the use of camera-traps strategically positioned near a corpse could uncover the frequency of such interactions. A data-collection protocol should include an ethogram detailing primary and secondary interactions (see Appendix S1–S4), describe the social and kin relationships and, particularly in case of dead-infant carrying, the cause of death, observation date, temperature/humidity, and parity and rank of the mother. Such data could be included in an online database to facilitate future comparisons.

There have also been many experimental paradigms that inform on how primates respond to dead individuals. Barrett & Behne (2005) suggest that disruptions of the body envelope could provide an important cue for death. Earlier applications and indirect evidence of this can be found in Hebb (1946) and Butler (1964). Since such responses occur in a violation-of-expectation scenario, using a looking-time paradigm in such experiments could prove effective. This could be achieved using video recordings and eye-tracking technology to challenge expectations of Causality and Irreversibility (i.e. simulated killing of a conspecific and it returning to life). Another method would be to play back calls of a recently deceased individual to members of its group (*sensu* Allen & Hauser, 1991; Palombit *et al*., 1997), for instance, bonobos can recognise recordings of a social partner even after years of separation (Keenan *et al*., 2016). Touch-screen matching-to-sample tasks depicting death and life as natural categories could demonstrate whether primates show any generalisation from subordinate to basic and superordinate category levels (i.e. dead conspecific to dead animal to decayed organic matter, respectively). Besides visual and audio modalities, olfaction could also play a role in determining these responses (Sarabian & MacIntosh, 2016; Wisman & Shrira, 2015) through scent and visual matching (i.e. rotten smell with dead animal picture). Given that the Animate/Inanimate distinction arises in different areas of the brain, it is unclear how corpses are represented. Neuro-imaging studies could provide insights into how primates process living and non-living entities (*sensu* Cross *et al*., 2013). Experimental methodologies should, of course, be devised to avoid distress or lasting harm to the animals (Prescott, 2010)

Many areas of inquiry remain, and whilst ethological reports are informative, resumption of experimental research methodologies confined within the ethical boundaries of animal research will be critical to advance the emerging field of primate thanatology.

## V. CONCLUSIONS

(1) Based on literature surveyed from the 19th century onwards, primates have long been observed performing thanatological behaviours, corroborated by independent present-day observations, such as grieving, carrying the dead, and protecting the body.

(2) Dead-infant carrying behaviour appears to represent part of a continuum of caretaking behaviours upon which natural selection has acted in the mammalian lineage. Such behaviours occur independent of the cause of death, although contextual and sensory cues to death might impact their duration. Whilst strepsirrhines and callitrichines do not engage in these behaviours, possibly due to postural/anatomical and behavioural constraints, the affective behaviours they exhibit towards their deceased infants are similar to other mammalian species.

(3) Dead adult and juvenile individuals engender greater attention from the group in comparison to dead infants. This not only depends on sex, rank and kinship of the dead individual but also on the social organisation of the group (multi-male/multi-female groups *versus* uni-male/multi-female groups).

(4) Behaviour towards dead group members includes direct interactions (hit, pull, groom, etc.). Depending on the context, some of these actions give the impression of attempts to rouse the corpse, while others may be attempts to monopolise the corpse or attacks on the dead individual's perceived failure to comply submissively to displays. Guarding the body, vigils, visitations, avoidance of the place of death and abandonment are among the typical behavioural features exhibited by primates.

(5) Vocalisations emitted during these interactions are usually alarm calls, distress cries and cohesion-related communication that signal both the internal emotional state and a danger assessment. The corpse of a conspecific triggers a set of behaviours consistent with a scenario of novelty/danger and violation-of-expectation whereupon a previously known group member ceases its agency.

(6) Primates appear to have an implicit awareness of death wherein the dead individual ceases its agency. Some observations suggest that they may be capable of Irreversibility and Causation. As a concept however, it is incomplete as individuals require frequent updates on the status of the dead (i.e. guarding, vigils, visitations). This could reflect attachment towards the dead conspecific confounding such awareness, as other individuals may cease rapidly to treat the individual as if it were alive.

(7) Our integrated model of life-death awareness proposes that primates are capable of at least two levels of death awareness. The first level is governed by perceptual categorisation, whilst the second is governed by associative concepts. A third level is governed by high-order reasoning (analogical/inductive/causal reasoning). Species possessing all these cognitive traits are in a likely position to acquire an emergent conceptual awareness of death similar to humans. Present cognitive research suggests that, among the primates, the great apes are the best candidates for such a position.

(8) Given their occurrence throughout the primate order, thanatological behaviours were likely to have been present in human ancestors from the Eocene through to the Pleistocene (45–3 mya). These examples of core mortuary behaviour would have persisted alongside emerging instances of archaic mortuary practices in the form of structured abandonment and funerary caching (3 mya–235 ka), culminating in the development of mortuary rituals such as formal burials (80–35 ka). The elaboration in thanatological behaviour during hominin evolution was accompanied by

cortical expansion and reorganisation as expressed in tool-making, control of fire and the emergence of language.

(9) Although thanatological interactions imply attachment relationships and could operate on the expectation the dead individual could recover, they may serve an evolutionary purpose by gathering information on the conspecific's state. Their additional role would be to promote a more rapid re-categorisation from living to dead, reduce costly vigilant/caregiving behaviours, be essential to the management of grieving responses, update ranks in the group's hierarchy, and accelerate the formation of new social bonds.

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## VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article

**Appendix S1.** Dead-infant carrying across non-human primates.

**Appendix S2.** Responses to dead/dying infants in strepsirrhines and callithrichines.

**Appendix S3.** Infant abandonment during violent deaths in non-human primates.

**Appendix S4.** Responses to dead juveniles and adults in non-human primates.

## Figure legends

**Fig. 1.** Publication frequency on the subject of primate thanatology from 1961 to 2017. The search was conducted in www.scholar.google.com using the key words: "dead"/"deceased" + "infant"/"conspecific" and the corresponding genus (i.e. *Macaca*, *Pan*).

**Fig. 2.** Dead-infant carrying across primate groups. (A) A ring-tailed lemur (*Lemur catta*) holds her infant in an awkward fashion (credit: Masayuki Nakamichi). (B) A northern muriqui (*Brachyteles hypoxanthus*) holding her infant on her hand whilst travelling (credit: Carla Possamai). (C) A stump-tailed macaque (*Macaca arctoides*) moves tripedally with her infant (credit: Aru Toyoda). (D) A chimpanzee (*Pan troglodytes*) crossing with her infant on her back (credit: Dora Biro).

**Fig. 3.** Dead-infant carrying behaviour distribution across primate taxa collected from single case reports ($N = 110$). Note: Papionini refers only to *Papio* and *Theropitecus* genera. See Appendix S1 for further details.

**Fig. 4.** A female crested macaque (*Macaca nigra*) hampers an attempt by another group member to inspect her dead infant. (credit: Andrew Walmsley).

**Fig. 5.** Cause of death in cases of dead-infant carrying collected from single case reports ($N = 110$). See Appendix S1 for further details.

**Fig. 6.** Segasira, a juvenile gorilla (*Gorilla b. beringei*) made a night nest and stayed close to its dead mother (Tuck) until the morning, grooming, resting against her and attempting to move her head (credit: Dian Fossey Gorilla Fund International - gorillafund.org).

**Fig. 7.** Sensory cues to death available to primates: a combination of the presence and absence of signals.

**Fig. 8.** Integrated model of life–death awareness. The first levels are governed by perceptual categorisation, whilst the second and third levels are governed by associative concept learning and high-order reasoning (analogical/inductive/causal reasoning), respectively. Species possessing all these cognitive processes are in a likely position to acquire an emergent conceptual awareness of death.

Table 1. Dead-infant carrying hypotheses.

| | |
|---|---|
| ***Unawareness hypothesis*** | The mother may be unaware or unsure that death has occurred, acting on error-management mode, suggesting it would be costlier, and ultimately non-adaptive, for her to abandon a temporarily unresponsive live infant, thus persisting on occasion in retaining a dead one (Alley, 1980; Nicolson, 1991; Hrdy, 2000). |
| ***Climate hypothesis*** | Climate may affect the duration of infant carrying since it impacts the preservation of the corpse (Matsuzawa, 1997; Fashing *et al*., 2011). This is strengthened by the argument that most prolonged carrying behaviours have been observed at high altitudes (Warren & Williamson, 2004; Lu *et al*., 2007; Fashing *et al*., 2011; Chai *et al*., 2013) or during dry conditions (Matsuzawa, 1997; Nakagawa, 2007; Biro *et al*., 2010). |
| ***Hormonal hypothesis*** | Following parturition, there is an activation of neuroendocrine systems: an interaction of the oxytocinergic, β-endorphin peptidergic and noradrenergic systems that promote and reinforce maternal behaviour, expressed in higher sensitivity to sensory signals from the newborn (Keverne, 1988). These hormones, which are crucial to mother–infant bonding, could also influence persistent *post-mortem* carrying by the mother (Kaplan, 1973; Biro *et al*., 2010). |
| ***Grief-management hypothesis*** | Carrying a dead infant may be a form of active grief-coping behaviour. The continued physical contact with the dead infant acts as an 'emotional buffer', relieving maternal distress and helping the mother adjust to the loss (Nicolson, 1991; for humans see also Cacciatore, J., Rådestad, I. & Frederik Frøen, J., 2008). |
| ***Infantile cues hypothesis*** | Dead infants retain infantile features (size/proportion, colouration, facial features) that make them attractive for females to carry them (Jay, 1962; Alley, 1980). |
| ***Learning-to-mother hypothesis*** | Nulliparous females's interest and willingness to carry dead infants positively impacts their maternal skills (Warren & Williamson, 2004). |
| ***Parity hypothesis*** | More experienced mothers (i.e. multiparous females) tend to carry dead infants for longer periods (Nishida, 2012; Sharma *et al*., 2011, but see Sugiyama *et al*., 2009). |
| ***Male-threat hypothesis*** | In baboons, although it is difficult to ascertain causal relationships, authors have made claims suggesting that males have threatened females who abandoned their dead infants, resulting in them |

| | |
|---|---|
| | carrying the infants again (Pollock, 1961; Hamburg, 1972). |

Table 2. Conceptual acquisition of death in humans[1].

| Subcomponent | Description | Age of acquisition |
|---|---|---|
| Irreversibility | Death is ultimately a permanent state | As early as age 3 |
| Universality | All living things are mortal | Ages 4–7 |
| Cessation | Biological and psychological functions terminate upon death | Ages 4–7 |
| Causation | Death is caused by internal and external factors ultimately leading to the breakdown of bodily functions | Ages 8–10 |

[1] Speece & Brent (1996); Kenyon (2001); Longbottom & Slaughter (2018).

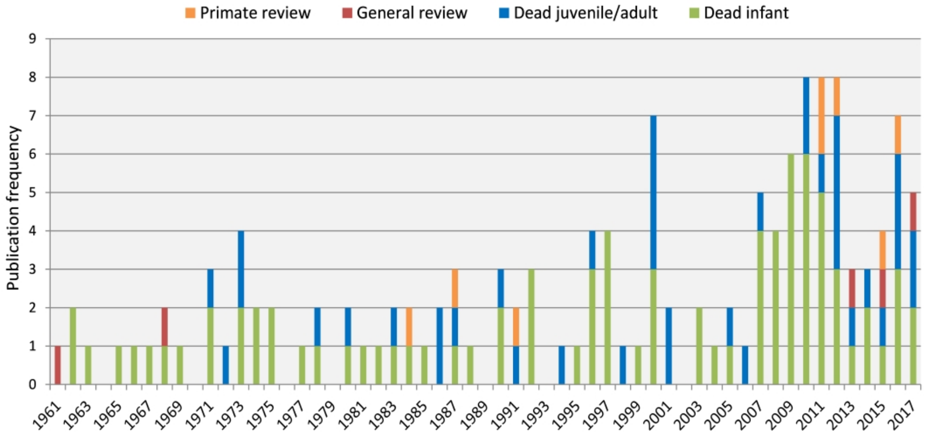


Figure 1. Publication frequency on the subject of primate thanatology from 1961 to 2017. The search was conducted in www.scholar.google.com using keywords: “dead”/”deceased” + “infant”/”conspecific” and the corresponding genus (i.e. *Macaca*, *Pan*).

Figure 2. Dead infant carrying across primate groups. Figure 2A. A ring-tailed lemur (*Lemur catta*) holds her infant in an awkward fashion (credit: Masayuki Nakamichi). Figure 2B. A northern muriqui (*Brachyteles hypoxanthus*) holding her infant on her hand whilst travelling (credit: Carla Possamai). Figure 2C. A stump-tailed macaque (*Macaca arctoides*) moves tripedally with her infant (credit: Aru Toyoda). Figure 2D. A chimpanzee (*Pan troglodytes*) crossing with her infant on her back (credit: Dora Biro).

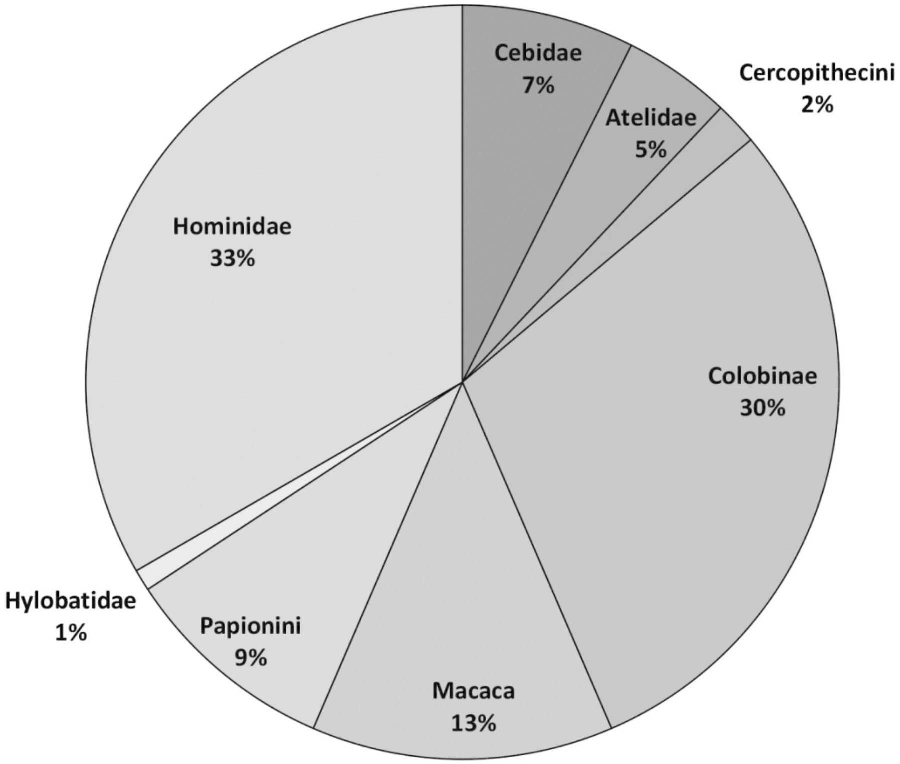


Figure 3. Dead-infant carrying behaviour distribution across primate taxa collected from single case reports (N = 110). Note: Papionini refers only to *Papio* and *Theropitecus* genera. See Appendix S1 for further details.

Figure 4. A female crested macaque (*Macaca nigra*) hampers an attempt of another group member to inspect her dead infant. (credit: Andrew Walmsley)

661x468mm (96 x 96 DPI)

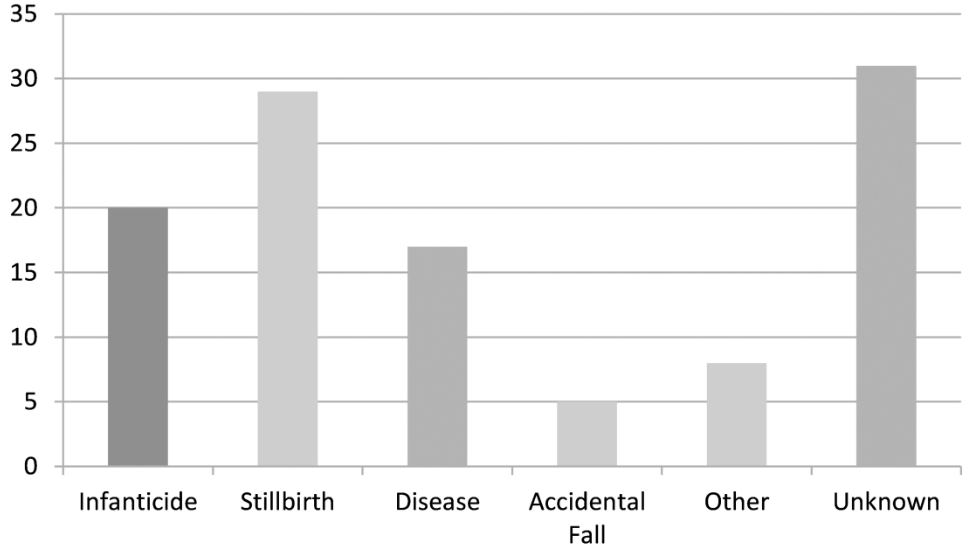


Figure 5. Cause of death in cases of dead-infant carrying collected from single case reports (N = 110). See Appendix S1 for further details.

Figure 6. Segasira, a juvenile (*Gorilla b. beringei*) made a night nest and stayed close to its dead mother (Tuck) until the morning, grooming, resting against her and attempting to move her head - (credit: Dian Fossey Gorilla Fund International - gorillafund.org).

352x236mm (72 x 72 DPI)

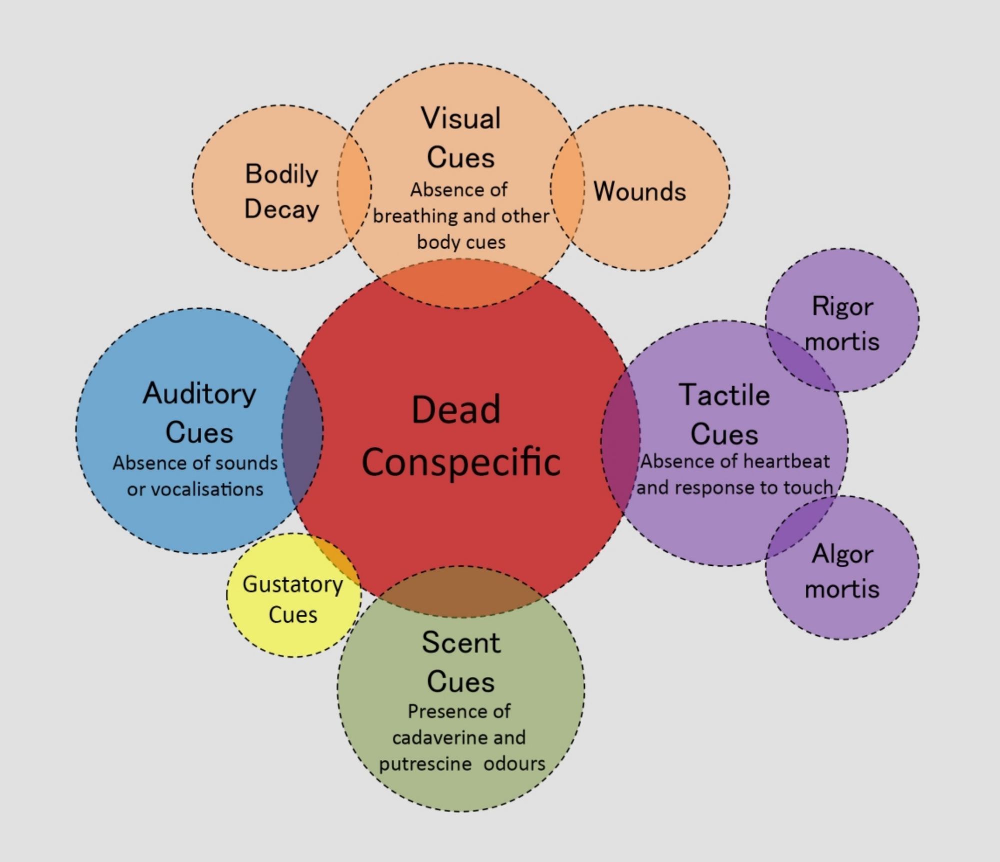
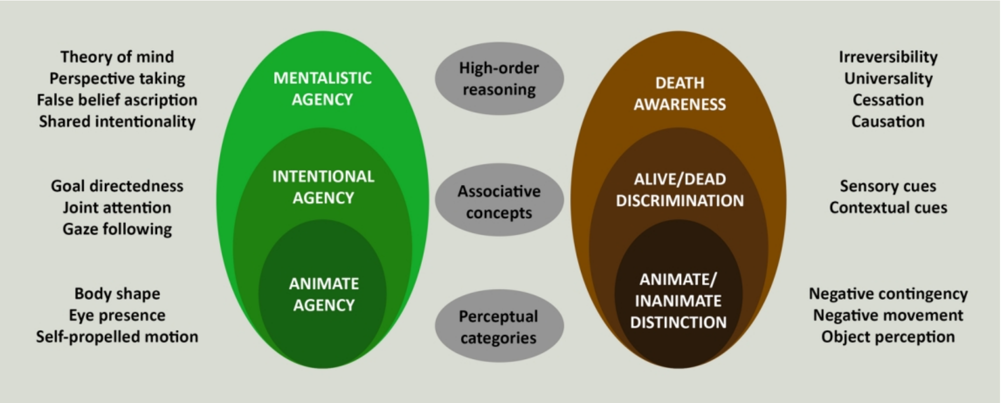


Figure 7. Sensory cues to death available to primates: a combination of the presence and absence of signals.



Integrated model of life–death awareness. The first levels are governed by perceptual categorisation, whilst the second and third levels are governed by associative concept learning and high-order reasoning (analogical/inductive/causal reasoning), respectively. Species possessing all these cognitive processes are in a likely position to acquire an emergent conceptual awareness of death.

137x55mm (300 x 300 DPI)

# **Appendix S1.** Dead-infant carrying across non-human primates

Table S1.1. Dead-infant carrying behaviour in New World monkeys

| Case | Species | Date | Carrying duration | Age of infant | Sex | Cause of death | Site | Season | Reference |
|---|---|---|---|---|---|---|---|---|---|
| N1 | *Cebus capucinus* | 24 Jan. 2009 | Hours | 88 days | ♀ | Infanticide | Guanacaste, Costa Rica | Dry | 1 |
| N2 | *Cebus capucinus* | 26 Apr. 2004 | < 1 day | 0 | ♂ | Stillbirth | Lomas-Barbudal, Costa Rica | Dry | 2 |
| N3 | *Cebus olivaceus* | 28 Apr. 1988 | ~50 min | days | N/A | Infanticide | Llanos, Venezuela | Wet | 3 |
| N4 | *Cebus olivaceus* | 27 May 1988 | > 2.30 hours | 9 months | ♀ | Infanticide | Llanos, Venezuela | Wet | 3 |
| N5 | *Sapajus nigritus* | 24 Nov. 2004 | 1 day | < week | N/A | Infanticide | Jaraguá, Brazil | Wet | 4 |
| N6 | *Sapajus nigritus* | 27 Jan. 2005 | 2 days | 8 weeks | ♂ | Infanticide | Iguazu N.P., Argentina | Wet | 5 |
| N7 | *Sapajus apella* | 8 Feb. 1991 | 2 days | 8 days | N/A | N/A | La Macarena N.P., Colombia | Dry | 6 |
| N8 | *Saimiri sciureus* | 29 Mar. 1964 | 6 weeks | 0 | N/A | Stillbirth | San Diego Zoo, U.S.A. (captive) | N/A | 7 |
| N9 | *Brachyteles hypoxanthus* | Apr. 1992 | ~5 days | 0 | ♂ | Stillbirth | Caratinga B.S., Brazil | Wet | 8 |
| N11 | *Brachyteles hypoxanthus* | 16 Aug. 2005 | 3 days | 1 day | ♂ | Premature | Caratinga B.S., Brazil | Dry | 9 |
| N10 | *Brachyteles arachnoides* | N/A | 4 days | N/A | N/A | N/A | Curitiba Zoo, Brazil (captive) | N/A | 10 |
| N12 | *Ateles geoffroyi* | 5 Jun. 2000 | <2 days | 3 weeks | ♂ | Infanticide | Punta Laguna, Mexico | Wet | 11 |
| N13 | *Alouatta seniculus* | 18 Jul. 2004 | 10 min | 0 | N/A | Stillbirth | Santa Rosa, Colombia | Wet | 12 |

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Table S1.2. Dead-infant carrying behaviour in Old World monkeys I

| Case | Species | Date | Carrying duration | Age of infant | Sex | Cause of death | Site | Season | Reference |
|---|---|---|---|---|---|---|---|---|---|
| O1 | *Papio h. anubis* | 16 Aug. 1970 | 2 days | 0 | ♂ | Stillbirth | Gombe N. P., Tanzania | Dry | 1 |
| O2 | *Papio h. ursinus* | Early Sep. 1994 | 10 days | 2 weeks | N/A | Infanticide | Cathedral Peak, South Africa | Temperate | 2 |
| O3 | *Papio h. cynocephalus* | 7 Nov. 1979 | 1 day | 8 days | ♂ | Kidnapping | Amboseli N. P., Kenya | Wet | 3 |
| O4 | *Papio h. cynocephalus* | 28/29 Apr. 1981 | 3-4 days | 0-2 yrs | N/A | Infanticide | Amboseli N. P., Kenya | Wet | 4 |
| O5 | *Papio h. cynocephalus* | 7 Nov. 2009 | 3 days | 11 days | ♀ | Disease | Amboseli N. P., Kenya | Wet | 5, 6 |
| O6 | *Papio h. hamadryas* | 17 Sep. 2002 | ~1 day | < 1 month | ♂ | Stillbirth | Awash N. P., Ethiopia | Wet | 7 |
| O7 | *Theropithecus gelada* | Winter 68-74 | 30 days | 0 | N/A | Stillbirth | Yerkes F.S., U.S.A. (captive) | N/A | 8 |
| O8 | *Theropithecus gelada* | 25 Apr. 1996 | 1 day | 0 | N/A | Stillbirth | Arsi, Ethiopia | Dry | 9 |
| O9 | *Theropithecus gelada* | 12 Feb. 1996 | 2 days | N/A | N/A | Infanticide | Arsi, Ethiopia | Dry | 9 |
| O10 | *Theropithecus gelada* | 1 Feb. 1996 | 3 days | N/A | N/A | Infanticide | Arsi, Ethiopia | Dry | 10 |
| O11 | *Rhinopithecus roxellana* | 3 Apr. 2005 | 35 days | 0 | ♂ | Stillbirth | Qinling Mountains, China | Wet | 11 |
| O12 | *Rhinopithecus roxellana* | 7 Oct. 2013 | 4.5 days | 183 days | ♂ | N/A | Qinling Mountains, China | Cool/wet | 12 |
| O13 | *Rhinopithecus roxellana* | 21 Nov. 2013 | 1 day | 220 days | ♀ | N/A | Qinling Mountains, China | Cold/dry | 12 |
| O14 | *Rhinopithecus roxellana* | 5 Apr. 2014 | 4 days | 0 | ♂ | Stillbirth | Qinling Mountains, China | Warm/wet | 12 |
| O15 | *Rhinopithecus roxellana* | 1 Jun. 2014 | 4-6 days | 0 | N/A | Stillbirth | Qinling Mountains, China | Warm/wet | 12 |
| O16 | *Rhinopithecus bieti* | 3 Apr. 2010 | ~4 days | 1 month | ♂ | N/A | Baimashueshan N. R., China | Dry | 13 |
| O17 | *Rhinopithecus bieti* | 14 Jan. 2011 | 1 day | 0 | N/A | Stillbirth | Baimashueshan N. R., China | Dry | 13 |
| O18 | *Rhinopithecus bieti* | 20 Sep. 2012 | 10 min | 5 months | ♂ | Infanticide | Shennongjia, China | Dry | 14 |
| O19 | *Colobus vellerosus* | 15 Nov. 2004 | 3 days | 3 days | ♂ | Infanticide | Boabeng-Fiema M.S., Ghana | Wet | 15 |
| O20 | *Colobus vellerosus* | 25 Nov. 2004 | 1 day | 1 day | N/A | Infanticide | Boabeng-Fiema M.S., Ghana | Wet | 15 |
| O21 | *Macaca mullata* | Spring, 1961 | 4 days | 0 | N/A | Stillbirth | Yerkes F.S. U.S.A. (captive) | N/A | 16 |
| O22 | *Macaca mullata* | 26 Dec. 1981 | 1 day | < 1 year | ♂ | Infanticide | Jackoo Forest, India | Dry | 17 |
| O23 | *Macaca m. tcheliensis* | 2 May 2012 | 26 days | <5 days | N/A | N/A | Mount Taihangshan, China | Wet | 18 |
| O24 | *Macaca radiata* | 5 Jul. 1996 | 4 days | ? | N/A | N/A | Wynaad W.S., India | Wet | 19 |
| O25 | *Macaca radiata* | 6 May. 2014 | 1.56 days | 0 | ♂ | Stillbirth | Chamundi Hill, India | Wet | 20 |
| O26 | *Macaca radiata* | 20 Oct. 2014 | 1.58 days | 6.6 months | ♂ | Electrocution | Chamundi Hill, India | Wet | 20 |
| O27 | *Macaca radiata* | 16 Dec. 2014 | 2.38 days | 7.8 months | ♀ | Electrocution | Chamundi Hill, India | Dry | 20 |
| O28 | *Macaca radiata* | 12 Nov. 2014 | 1.67 days | 5.2 months | ♂ | Disease | Chamundi Hill, India | Dry | 20 |
| O29 | *Macaca silenus* | 27 Jun. 2014 | 1.65 days | 4.5 months | ♀ | Disease | Valparai, India | Wet | 20 |
| O30 | *Macaca thibetana* | 27 Mar. 2007 | 9 days | 0 | ♀ | Stillbirth | Huangxan Fuxi, China | Temperate | 21 |
| O31 | *Macaca cyclopis* | 26 May 2007 | 2 days | 0 | N/A | Stillbirth | Mt. Chai, Taiwan | Wet | 22 |
| O32 | *Macaca fuscata* | 2011 | 29 days | ? | ? | N/A | Inuyama, Japan (captive) | N/A | 23 |
| O33 | *Macaca fuscata* | 2013 | 28 days | ? | ? | N/A | Inuyama, Japan (captive) | N/A | 23 |
| O34 | *Macaca tonkeana* | 8 Mar. 2017 | 25 days | 4 days | N/A | N/A | Parco Faunistico, Italy (captive) | N/A | 24 |
| O35 | *Trachypithecus geei* | N/A | 3 days | 0 | N/A | N/A | Sepahijala, W.S. India | N/A | 25 |
| O36 | *Erythrocebus patas* | N/A | 27 days | 0 | N/A | Stillbirth | Kala Maloue, Cameroon | Dry | 26 |
| O37 | *Erythrocebus patas* | N/A | 1 day | 0 | N/A | Stillbirth | Kala Maloue, Cameroon | Dry | 26 |
| O38 | *Semnopithecus entellus* | N/A | 5 days | 8 months | N/A | N/A | Captive | N/A | 27 |

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Table S1.3. Dead-infant carrying behaviour in Old World monkeys II (combined data from the Jodpur site)

| Case | Species | Date | Carrying duration | Age of infant | Sex | Cause of death | Site | Season | Reference |
|---|---|---|---|---|---|---|---|---|---|
| L1 | *Semnopithecus entellus* | 23 Sep. 1983 | 2 days | 0 | ♀ | Stillbirth | Jodpur, India | Wet | 1 |
| L2 | *Semnopithecus entellus* | 13 Jun. 1984 | 1.5 hours | 9 months | ♀ | Accidental | Jodpur, India | Wet | 1 |
| L3 | *Semnopithecus entellus* | 17 Jun. 1985 | 3 days | 23 days | ♂ | Accidental | Jodpur, India | Wet | 1 |
| L4 | *Semnopithecus entellus* | 28 Dec. 1985 | 3 hours | 0 | ♂ | Stillbirth | Jodpur, India | Dry | 1 |
| L5 | *Semnopithecus entellus* | 8 Jan. 1986 | 1 day | 0 | ♀ | Stillbirth | Jodpur, India | Dry | 1 |
| L6 | *Semnopithecus entellus* | 15 Sep. 1987 | 1 hour | 7 months | ♀ | Accidental | Jodpur, India | Wet | 1 |
| L7 | *Semnopithecus entellus* | 18 Jun. 1989 | 1 day | 0 | ♂ | Stillbirth | Jodpur, India | Wet | 1 |
| L8 | *Semnopithecus entellus* | 24 Jan. 1990 | 1 day | 1 | ♀ | N/A | Jodpur, India | Dry | 1 |
| L9 | *Semnopithecus entellus* | 19 Feb. 1990 | 2 days | 4 | ♂ | N/A | Jodpur, India | Dry | 1 |
| L10 | *Semnopithecus entellus* | 28 Oct. 1994 | 2 days | 65 days | ♂ | N/A | Jodpur, India | Dry | 1 |
| L11 | *Semnopithecus entellus* | 11 May 1995 | 1 day | 15 days | ♀ | N/A | Jodpur, India | Dry | 1 |
| L12 | *Semnopithecus entellus* | 31 Mar. 1996 | 1 day | 2 months | N/A | N/A | Jodpur, India | Dry | 1 |
| L13 | *Semnopithecus entellus* | Aug. 2008 | 27 days | 3 months | N/A | N/A | Jodpur, India | Wet | 2 |
| L14 | *Semnopithecus entellus* | Sep. 2008 | 10 days | 2 months | N/A | N/A | Jodpur, India | Wet | 2 |
| L15 | *Semnopithecus entellus* | Oct. 2008 | 8 days | 3 months | N/A | N/A | Jodpur, India | Dry | 2 |
| L16 | *Semnopithecus entellus* | Feb. 2009 | 4 days | 0 | N/A | Stillbirth | Jodpur, India | Dry | 2 |
| L17 | *Semnopithecus entellus* | Mar. 2009 | 7 days | 0 | N/A | Stillbirth | Jodpur, India | Dry | 2 |
| L18 | *Semnopithecus entellus* | Nov. 2009 | 3 days | 0 | N/A | Stillbirth | Jodpur, India | Dry | 2 |
| L19 | *Semnopithecus entellus* | Dec. 2009 | 6 days | 5 months | N/A | Mishandling | Jodpur, India | Dry | 2 |
| L20 | *Semnopithecus entellus* | Jan. 2010 | 17 days | 3 months | N/A | N/A | Jodpur, India | Dry | 2 |
| L21 | *Semnopithecus entellus* | May 2010 | 9 days | 4 months | N/A | N/A | Jodpur, India | Dry | 2 |
| L22 | *Semnopithecus entellus* | Jun. 2010 | 3 days | 1 month | N/A | N/A | Jodpur, India | Wet | 2 |

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Table S1.4. Dead-infant carrying behaviour in lesser and great apes

| Case | Species | Date | Carrying Duration | Age | Sex | Cause of Death | Site | Season | Reference |
|---|---|---|---|---|---|---|---|---|---|
| A1 | *Hylobates syndactilus* | Aug. 1987 | Minutes | 0 | ♂ | Stillbirth | Ketambe, R.C., Indonesia | Dry | 1 |
| A2 | *Pongo abelii* | 21 May 2007 | 10 days | 12 months | N/A | N/A | Bukit Lawang, Indonesia | Dry | 2 |
| A3 | *Pongo abelii* | 9 Jun. 2007 | 4 days | 9 months | N/A | N/A | Bukit Lawang, Indonesia | Dry | 2 |
| A4 | *Gorilla b. beringei* | N/A | 4 days | N/A | N/A | N/A | Kabara, Albert N.P., Congo | N/A | 3 |
| A5 | *Gorilla b. beringei* | 24 Feb. 1967 | 4 days | 1 day | ♂ | Infanticide | Karisoke R.C., Rwanda | Wet | 4 |
| A6 | *Gorilla b. beringei* | 10 May 1986 | 2 days | 7 days | ♀ | Disease | Karisoke R.C., Rwanda | Wet | 5 |
| A7 | *Gorilla b. beringei* | N/A | 2 days | 6 weeks | ♀ | Infanticide | Karisoke R.C., Rwanda | N/A | 6 |
| A8 | *Gorilla b. beringei* | Apr. 1996 | 6 days | 36 days | N/A | Infanticide | Volcanoes N. P., Rwanda | Wet | 7 |
| A9 | *Gorilla b. beringei* | May. 1996 | 20 days | 13 days | N/A | Infanticide | Volcanoes N. P., Rwanda | Wet | 7 |
| A10 | *Gorilla b. graueri* | Dec. 2003 | 7 days | < 5 days | N/A | Infanticide | Kahuzi-Biega N. P., D.R. Congo | Dry | 8 |
| A11 | *Pan paniscus* | N/A | ~2 days | 1 year | ♀ | N/A | Wamba, Congo | N/A | 9 |
| A12 | *Pan paniscus* | 9 Jul. 2008 | 1 day | 2.5 years | ♀ | N/A | Lui Kotale, Congo | Dry | 10 |
| A13 | *Pan troglodytes* | ~13 Feb. 1965 | ~1 day | 3 months | ♀ | Accidental | Gombe, Tanzania | N/A | 11 |
| A14 | *Pan troglodytes* | ~14 Sep. 1966 | 4 days | 4 months | ♂ | Disease | Gombe, Tanzania | Dry | 11 |
| A15 | *Pan troglodytes* | Sep. 1974 | ~2 days | 1-2 dats | N/A | Infanticide | Gombe, Tanzania | Dry | 12 |
| A16 | *Pan troglodytes* | 4 May 2007 | ~3 days | 0 | N/A | Stillbirth | Gombe, Tanzania | Wet | 13 |
| A17 | *Pan troglodytes* | 25 Sep. 2006 | ~2 days | 5 months | N/A | N/A | Gombe, Tanzania | Dry | 13 |
| A18 | *Pan troglodytes* | 23 Mar. 1991 | >1 day | 2 years | ♂ | Accidental | Täi Forest, Ivory Coast | Wet | 14 |
| A19 | *Pan troglodytes* | N/A | >1 day | 14 months | ♂ | Disease | Täi Forest, Ivory Coast | N/A | 15, 16 |
| A20 | *Pan troglodytes* | 24 Jan. 1992 | >27 days | 2.5 years | ♀ | Disease | Bossou, Guinea | Dry | 17 |
| A21 | *Pan troglodytes* | 27 Nov. /2 Dec. 2003 | ~68 days | 1.2 years | ♂ | Disease | Bossou, Guinea | Dry | 18 |
| A22 | *Pan troglodytes* | 29/30 Dec. 2003 | ~19 days | 2.6 years | ♀ | Disease | Bossou, Guinea | Dry | 18 |
| A23 | *Pan troglodytes* | 18 May 2010 | 1 day | 1.3 years | ♀ | Disease | Chimfunshi, Zambia (captive) | N/A | 19 |
| A24 | *Pan troglodytes* | 6 Aug. 1968 | > 90 days | 2 years | ♂ | Injury | Mahale, Tanzania | Dry to Wet | 20 |
| A25 | *Pan troglodytes* | Aug. 1971 | N/A | 1 year | ♂ | Injury | Mahale, Tanzania | Dry | 20 |
| A26 | *Pan troglodytes* | May, 1977 | N/A | 2 months | ♂ | Disease | Mahale, Tanzania | Temperate | 21 |
| A27 | *Pan troglodytes* | 1 Sep. 1992 | 1 day | 3 years | ♀ | Injury | Mahale, Tanzania | Dry | 22 |
| A28 | *Pan troglodytes* | 13 May 1993 | 7 days | < 3 weeks | ♂ | N/A | Mahale, Tanzania | Temperate | 23 |
| A29 | *Pan troglodytes* | 15 May, 1993 | 26 days | < 2 months | ♂ | Disease | Mahale, Tanzania | T. to Dry | 23 |
| A30 | *Pan troglodytes* | 11 Oct, 1993 | 111-142 days | ~4 months | ♂ | Disease | Mahale, Tanzania | T. to Wet | 23 |
| A31 | *Pan troglodytes* | 21 Oct, 1993 | 7 days | 3.5 months | ♂ | Disease | Mahale, Tanzania | Temperate | 23 |
| A32* | *Pan troglodytes* | 19 Oct. 1993 | > 2 hours | < 3 days | ♂ | Infanticide/stillbirth | Mahale, Tanzania | Temperate | 23 |
| A33 | *Pan troglodytes* | 13 Nov. 1993 | < a night | ~4 months | ♀ | Disease | Mahale, Tanzania | Wet | 23 |
| A34 | *Pan troglodytes* | 1 Jul. 2006 | 22 days | 1 year | ♀ | Disease | Mahale, Tanzania | Wet | 23 |
| A35 | *Pan troglodytes* | 15 Jul. 2006 | 90 days | 1 year | ♀ | Disease | Mahale, Tanzania | Dry | 24 |
| A36 | *Pan troglodytes* | 10 Oct. 2008 | < 2 days | 0 | ♂ | Stillbirth | Mahale, Tanzania | Temperate | 25 |
| A37 | *Pan troglodytes* | 10 Oct. 2008 | 2 days | 0 | ♂ | Stillbirth | Mahale, Tanzania | Temperate | 25 |

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*Case not counted as infanticide.

# **Appendix S2.** Responses to dead/dying infants in Strepsirrhines and Callithrichines.

Table S2.1. Responses to dead/dying infants in strepsirrhines

| Case | Species | Date | Ambivalence Duration | Age of Infant | Sex | Cause of Death | Site | Season | Reference |
|---|---|---|---|---|---|---|---|---|---|
| S1 | *Propithecus verrauxi* | 12 Oct. 2007 | 16 min | 3 months | ♂ | Infanticide | Beza Mahafali, S.R., Madagascar | Dry | 1 |
| S2 | *Propithecus verrauxi* | 26 Oct. 2007 | 54 min | 3 months | ♀ | Infanticide | Beza Mahafali, S.R., Madagascar | Dry | 1 |
| S3 | *Lemur catta* | 9 Oct. 2009 | 160 min | N/A | N/A | Injury | Bealoka Forest, Madagascar | Dry | 2 |
| S4 | *Lemur catta* | 28 Oct. 1994 | ~4 hours | 2/3 days | ♀ | Environmental stress | Berenty Reserve. Madagascar | Dry | 3 |
| S5 | *Lemur catta* | 9 Oct. 1994 | >3 hours | 4/6 days | ♂ | Environmental stress | Berenty Reserve. Madagascar | Dry | 3 |
| S6 | *Lemur catta* | 25 Sep. 1995 | 2 hours | 18 days | ♂ | Environmental stress | Berenty Reserve. Madagascar | Dry | 3 |
| S7 | *Lemur catta* | 1 Oct. 1994 | 90 min | 21/23 days | ♀ | Environmental stress | Berenty Reserve. Madagascar | Dry | 3 |
| S8 | *Lemur catta* | 3 Oct. 1994 | 4h20min | 24 days | ♀ | Environmental stress | Berenty Reserve. Madagascar | Dry | 3 |
| S9 | *Lemur catta* | 6 Oct. 1994 | ~7 hours | 25/27 days | ♂ | Environmental stress | Berenty Reserve. Madagascar | Dry | 3 |
| S10 | *Lemur catta* | 10 Nov. 1994 | <8 hours | 25/27 days | ♂ | Environmental stress | Berenty Reserve. Madagascar | Wet | 3 |

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Table S2.2. Responses to dead/dying infants in callithrichines

| Case | Species | Date | Ambivalence Duration | Age | Sex | Cause of Death | Site | Season | Reference |
|---|---|---|---|---|---|---|---|---|---|
| C1 | *Callithrix jacchus* | Mar. 1992 | 1 hour | 24 days | ♀ | Infanticide | Nisia Forest, Brazil | Wet | 1 |
| C2 | *Callithrix jacchus* | Jan. 1987 | 135 min | 0 | ♂ | Accidental | Santo Antonio Ranch, Brazil | Dry | 2 |
| C3 | *Callithrix jacchus* | 13 Apr. 1997 | N/A (hours) | 3 days | N/A | Accidental | Nisia Forest, Brazil | Wet | 3 |
| C4 | *Callithrix jacchus* | N/A | 312 min | N/A | N/A | Accidental | Tapacurá F.S., Brazil | N/A | 4 |
| C5 | *Callithrix flaviceps* | 15 Nov. 2008 | 122 min | 1 day | N/A | Infanticide | Augusto Ruschi B.R. e, Brazil | Wet | 5 |
| C6 | *Saguinus mystax* | 15 Aug. 2007 | 18 min | 2 weeks | ♂ | Infanticide | Quebrada Branco E. B., Peru | Dry | 6 |
| C7 | *Saguinus mystax* | 8 Mar. 2008 | 81 min | N/A | N/A | Accidental | Quebrada Branco E. B., Peru | Dry | 6 |

1. Digby, L. (1995). 2. Roda, S. A. & Pontes, A. R. M. (1998). 3. Lazaro-Perea, C., *et al*. (2000). 4. Thompson, C. L., *et al.* (2018). 5. Hilário, R. R. & Ferrari, S. F. (2010). 6. Culot, L., *et al*. (2011).

# **Appendix S3.** Infant abandonment during violent deaths in non-human primates.

Table S3.1. Infant abandonment during violent deaths

| Case | Species | Date | Desertion | Age | Sex | Cause of Death | Site | Season | Reference |
|---|---|---|---|---|---|---|---|---|---|
| K1 | *Cebus olivaceus* | 11 Jul. 1987 | After death | ~7 days | ♂ | Infanticide | Llanos, Venezuela | Wet | 1 |
| K2 | *Cebus capucinus* | 30 Aug. 2008 | After death | 69 days | ♀ | Infanticide | Guanacaste, Costa Rica | Wet | 2 |
| K3 | *Alouatta arctoidea* | 27 Apr. 1990 | After injury | 1.5 months | N/A | Infanticide | Guarico, Venezuela | Wet | 3 |
| K4 | *Alouatta arctoidea* | 22 Dec. 1990 | After death | 2 days | N/A | Infanticide | Guarico, Venezuela | Dry | 3 |
| K5 | *Alouatta arctoidea* | 29 Apr. 1990 | After death | 1.5 months | N/A | Infanticide | Guarico, Venezuela | Wet | 3 |
| K6 | *Alouatta arctoidea* | 1 Mar. 1991 | After death | 6 days | N/A | Infanticide | Guarico, Venezuela | Dry | 3 |
| K7 | *Alouatta arctoidea* | 15 Dec. 1989 | After injury | 8.5 months | ♂ | Infanticide | Guarico, Venezuela | Dry | 3 |
| K8 | *Alouatta pigra* | 26 Feb. 2010 | After death | 1/2 weeks | ♂ | Infanticide | Palenque N.P. Mexico | Dry | 4 |
| K9 | *Alouatta pigra* | 27 Feb. 2010 | After injury | 1/2 Weeks | ♀ | Infanticide | Palenque N.P. Mexico | Dry | 4 |
| K10 | *Alouatta pigra* | 28 Feb. 2010 | After death | 3 months | ♀ | Infanticide | Palenque N.P. Mexico | Dry | 4 |
| K11 | *Alouatta pigra* | N/A | After injury | 15 days | ♂ | Infanticide | Balancan, Mexico | N/A | 5 |
| K12 | *Alouatta palliata* | Aug. 1980 | After injury | 4.5 months | ♂ | Infanticide | Guanacaste, Costa Rica | Wet | 6 |
| K13 | *Ateles belzebuth* | 10 May. 2006 | After death | 4 weeks | ♂ | Infanticide | Cocha Cachu, Peru | Dry | 7 |
| K14 | *Ateles seniculus* | 16 Aug. 2010 | After death | 0 | ♂ | Infanticide | San Juan, Colombia | Dry | 8 |
| K15 | *Ateles seniculus* | 30 Jun. 2011 | After injury | N/A | N/A | Infanticide | San Juan, Colombia | Dry | 8 |
| K16 | *Ateles geoffroy* | 21 Jan. 2014 | After injury | 15 months | ♂ | Infanticide | Runaway Creek, Belize | Dry | 9 |
| K17 | *Cercopithecus mitis* | N/A | After death | 5.8 months | ♀ | Infanticide | Hannover Zoo, Germany (captive) | N/A | 10 |
| K18 | *Cercopithecus mitis* | 16 Sep. 1993 | After death | N/A | N/A | Infanticide | Budongo F.R., Uganda | Wet | 11 |
| K19 | *Cercopithecus mitis* | 6 Apr. 2004 | After death | 55 days | N/A | Infanticide | Kakamega Forest, Kenya | Wet | 12 |
| K20 | *Cercopithecus mitis* | 10 Jul. 2008 | After death | 22 days | N/A | Infanticide | Kakamega Forest, Kenya | Wet | 12 |
| K21 | *Cercopithecus mitis* | 24 Jul. 2008 | After death | N/A | N/A | Infanticide | Kakamega Forest, Kenya | Wet | 12 |
| K22 | *Cercopithecus ascanius* | 23 Nov. 1975 | After death | 0 | N/A | Infanticide | Kibale Forest, Uganda | Wet | 13 |
| K23 | *Colobus badius* | 31 May. 1982 | After death | 29 days | ♂ | Infanticide | Kibale Forest, Uganda | Wet | 14 |
| K24 | *Colobus guereza* | 20 Jun. 1996 | After death | 1 day | ♀ | Infanticide | Kibale N.P., Uganda | Dry | 15 |
| K25 | *Colobus vellerosus* | 25 Mar. 2004 | After death | 137 days | ♀ | Infanticide | Boabeng-Fiema M.S., Ghana | Dry | 16 |
| K26 | *Semnopithecus entellus* | 3 Feb. 1983 | After injury | 58 days | ♂ | Infanticide | Jodpur, India | Dry | 17 |
| K27 | *Semnopithecus entellus* | 9 Feb. 1983 | After injury | 103 days | ♀ | Infanticide | Jodpur, India | Dry | 17 |
| K28 | *Semnopithecus entellus* | 11 Feb. 1983 | After injury | 140 days | ♂ | Infanticide | Jodpur, India | Dry | 17 |
| K29 | *Semnopithecus entellus* | 10 Jul. 1982 | After injury | 33 days | ♂ | Infanticide | Jodpur, India | Wet | 18 |
| K30 | *Semnopithecus entellus* | 18 Apr. 1981 | After death | N/A | N/A | Infanticide | Jodpur, India | Dry | 19 |
| K31 | *Semnopithecus entellus* | 19 Apri. 1981 | After death | N/A | N/A | Infanticide | Jodpur, India | Dry | 19 |
| K32 | *Rhinopihecus bieti* | 31 Dec. 2009 | After injury | 8 months | ♂ | Infanticide | Wild Animal Park, China (captive) | Dry | 20 |
| K33 | *Macaca fuscata* | 1 Dec. 1998 | After injury | N/A | ♀ | Infanticide | Yakushima, Japan | Dry | 21 |
| K34 | *Hylobates hoolock* | 17 Oct. 1985 | After injury | 0 | ♂ | Infanticide | Meghalaya, India | Dry | 22 |
| K35 | *Gorilla beringei* | 5 Dec. 1978 | After death | 8 months | ♀ | Infanticide | Karisoke R. C., Rwanda | Dry | 23 |
| K36 | *Pan troglodytes* | Aug. 1975 | After death | 3 weeks | ♀ | Infanticide | Gombe, Tanzania | Dry | 24 |
| K37 | *Pan troglodytes* | 29 Sep. 1995 | After death | < week | ♂ | Infanticide | Budongo F.R., Uganda | Dry | 25 |
| K38 | *Pan troglodytes* | 3 Apr. 1999 | After death | N/A | N/A | Infanticide | Kibale N.P., Uganda | Wet | 26 |
| K39 | *Pan troglodytes* | 28 Jun. 1999 | After death | N/A | N/A | Infanticide | Kibale N.P., Uganda | Dry | 26 |
| K40* | *Macaca radiata* | 23 Mar. 2014 | After death | 2 days | N/A | Mishandling | Chamundi Hills, India | Dry | 27 |
| K41* | *Macaca radiata* | N/A | After death | 21 months | ♂ | Electrocution | Chamundi Hills, India | N/A | 27 |
| K42* | *Nasalis larvatus* | 21 Jul. 2005 | After death | 10 months | ♂ | Predation | Sabah, Malaysia | Dry | 28 |
| K43* | *Nasalis larvatus* | 8 Apr. 2006 | After death | 1.5 years | ♀ | Predation | Sabah, Malaysia | Dry | 28 |

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*Case not included in section III.1e

## **Appendix S4.** Responses to dead juveniles and adults in non-human primates.

Table S4.1. Responses to dead juveniles and adults

| | | | Direct Interactions | | | | | | | | | | Secondary Interactions | | | Social Interactions | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **Sex** | **Cause** | **Peer** | **Grooming** | **Poke** | **Gentle Touch** | **Rough Touch** | **Bite** | **Pull/Drag** | **Object Contact** | **Swat Bugs** | **Sniffing** | **Guard/Mob** | **Vigil** | **Revisit** | **Distress /Calls** | **Display** | **Play** | **Sex** | **Grooming** | **Grief Signs** | **Reassurance** | **Reference** |
| *Pan troglodytes* | O ♀ | Accidental | X | X | X | X | X | | X | | | | | | X | X | X | | | | | | 1 |
| *Pan troglodytes* | A ♂ | Accidental | X | | | | | | | | | | | | | X | X | | X | X | | X | 2 |
| *Pan troglodytes* | O ♀ | Natural | X | X | | X | X | | | | | | | X | | | X | | | X | X | | 3 |
| *Pan troglodytes* | O ♀ | Natural | | X | | X | | | X | | | | | X | | | | | | | | | 4 |
| *Pan troglodytes* | A ♂ | Disease | | | | X | | | X | | | | | | | | | | | | X | | 5 |
| *Pan troglodytes* | A ♀ | Accidental | X | | | X | X | | | X | | | | | | X | | | | X | | X | 6 |
| *Pan troglodytes* | J ♀ | Predation | X | X | | X | | | X | | | X | X | | | X | | X | | | | | 7 |
| *Pan troglodytes* | O ♂ | Killing | X | | | X | X | X | | | | | | X | X | X | X | | | | | | 8 |
| *Pan troglodytes* | J ♂ | Disease | X | X | | X | X | | | X | | X | | X | | | X | | | | | | 9 |
| *Pan troglodytes* | A ♂ | Killing | X | X | X | X | X | | X | X | X | X | | | | X | X | | | X | | X | 10 |
| *Pan troglodytes* | J ♀ | Accidental | X | X | | X | | | X | | X | | | | | | X | | | | | | 11 |
| *Pan troglodytes* | A ♂ | Killing | X | | | | | X | | | | | | | | X | | | | | | | 12 |
| *Gorilla beringei* | O ♀ | Natural | | X | X | X | X | | X | | | | | | | | X | | | | | | 13 |
| *Gorilla gorilla* | O ♂ | Natural | | | X | | | | | | | X | | X | X | X | | | | | X | | 14 |
| *Gorilla gorilla* | A ♀ | Disease | | | | X | | | | | | | | X | | | | | | | | | 15 |
| *Gorilla gorilla* | A ♀ | Disease | | | | X | | | | X | | | | X | | X | X | | | | | | 15 |
| *Papio anubis* | A ♂ | Predation | X | | | X | | | | | | X | | X | | X | | | | | | | 16 |
| *Macaca mulatta* | A ♂ | Killing | X | X | | | | X | X | | | X | | | | X | X | | X | X | | | 17 |
| *Macaca sylvanus* | A ♀ | Accidental | X | X | | X | | | | | | | X | X | X | X | | | | | | | 18 |
| *Macaca sylvanus* | J ♂ | Accidental | X | | | | | | X | | | | X | X | | | | | | | | | 18 |
| *Trachypithecus phayrei* | A ♀ | Accidental | | X | | X | | | X | | | | x | | | | | | | | | | 19 |
| *Rhinopithecus bieti* | O ♀ | Accidental | X | X | | X | | | X | | | X | | X | X | X | | X | | X | | | 20 |
| *Callithrix jacchus* | A ♀ | Accidental | X | | | X | | | | | | X | X | X | | X | | | | | | | 21 |
| *Propithecus sp.* | A ♂ | Predation | X | | | | | | | | | | | X | X | X | | | | | | | 22 |

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