Reinvention: an International Journal of Undergraduate Research 17:1 (2024)

A Concept of Death in Genus *Pan*: Implications for Human Evolution

Katherine H. McLean, University of Auckland

Abstract

An understanding of what death and dying entail is termed a concept of death (CoD), and the human CoD is often viewed as one of the characteristics that distinguishes our species. In this research, I identified an analogous understanding of death and dying in our closest living relatives—genus *Pan*. Linguistic frameworks designed for studying the CoD in human children look for evidence of understanding of several facets of death. I adapted these frameworks for the non-verbal *Pan* species, systematically analysing written and video recordings of chimpanzee and bonobo behaviours surrounding death within these new behavioural frameworks. I identified compelling evidence for the comprehension of several aspects of death, and thus for the presence of a human-like CoD in chimpanzees and bonobos. This has implications for our own evolutionary story and raises questions about what makes humans 'human'.

Keywords: Biological anthropology; evolutionary anthropology; evolutionary biology; primatology; genus *Pan*; thanatology; primate mortuary behaviour; concept of death.

A concept of death in genus *Pan*: Implications for human evolution

The human understanding of death has long been viewed as one of the characteristics that helps distinguish our species (Gonçalves & Biro, 2018). This understanding of what death and dying entail is termed the concept of death (CoD), and opinions vary regarding the extent of the CoD in the broader animal kingdom (Anderson, 2016; Gonçalves & Biro, 2018; Monsó & Osuna-Mascaró, 2020). During childhood, humans develop a complex CoD that involves comprehending both the biological nature of death and its more metaphysical aspects (Kenyon, 2001; Speece & Brent, 1984, 1992). The critical evolutionary question is how early in our lineage this CoD evolved—whether it is restricted to modern humans, genus *Homo*, or more widely present in primates. Suppose we had reason to believe that the CoD evolved early in our evolutionary lineage. This could help contextualise early hominin behaviours, offer alternate meanings to findings in the fossil record, and spur a rethink of pre-*sapiens* burials. Possible cases of pre-*sapiens* deliberate burials are currently disputed; however, the earlier in our lineage that the CoD evolved, the higher the likelihood that possible burials or corpse disposals in extinct species of genus *Homo* may have represented intentional funerary practises. The fossil record is not often well-suited to behavioural research; hence the most logical step from a comparative evolutionary perspective is to study our closest living relatives—the two living members of the genus *Pan*. Suppose a human-like CoD is present in the chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*). In that case, it is probable that the CoD was also possessed by the last common ancestor of chimpanzees, bonobos, and humans (CHLCA), as well as early hominins (de Waal, 2019; Gruber & Clay, 2016; Suddendorf, 2004). In this paper, I thus investigate the extent of a human-like CoD in *Pan*, using a framework adapted from studies on the development of the CoD in human children to analyse *Pan* mortuary behaviours.

Chimpanzee and bonobo sociality and behavioural flexibility

It is necessary to understand the nature of *Pan* sociality and relationships, since this may be intimately related to the CoD. The chimpanzee and the bonobo are morphologically and physiologically very similar (de Waal, 1995). They both form large multi-male and multi-female social groups with specific home territories (Boesch *et al.*, 2008; Stanford, 1998). All members of genus *Pan* are highly interested in genitals, with conspecific interactions often involving genital inspection, smelling, and grooming (de Waal, 1995, 2019; Stanford, 1998; van Lawick-Goodall, 1968). Their interest in genitals is second only to their interest in faces (van Lawick-Goodall, 1968; van Leeuwen *et al.*, 2016). Chimpanzees and bonobos share fission-fusion social systems, where subgroups split up to forage or travel during the day and re-join at night (Aureli *et al.*, 2008; Furuichi, 2011). Males may also move around on their own outside subgroups (van Lawick-Goodall, 1968). The everyday relationships of chimpanzees and bonobos often reach a depth of 'bondedness' found only in reproductive pairbonds in other social birds and mammals (Dunbar & Shultz, 2007).

However, some social behaviours differ substantially between the two species (Gruber & Clay, 2016; Pruetz *et al.*, 2017). Chimpanzees form patriarchal groups led by a single alpha male (de Waal, 1995, 2019). The male hierarchy within these groups is dynamic and competitive (de Waal, 2019), whereas, in the secondary female hierarchy, age is most powerful (Foerster *et al.*, 2007). Sometimes the highest-ranked female can outrank the lowest-ranked male, but this is extremely unusual (de Waal, 1995; van Lawick-Goodall, 1968). Violence and aggression are common in chimpanzee groups (Hare *et al.*, 2012; Pruetz *et al.*, 2017)—expressed both intracommunity, via dominance displays and other hierarchy maintenance (de Waal, 1995; van Leeuwen *et al.*, 2016), and intercommunity, via boundary patrols and coalitionary attacks (Boesch *et al.*, 2008; de Waal, 1995; Pruetz *et al.*, 2017). Whilst males are highly territorial (Boesch *et al.*, 2008), females leave their natal group as they near sexual maturation (de Waal, 1995; Stanford, 1998). The strongest bonds in chimpanzee troops are consequently between males (de Waal, 1995; Pepper *et al.*, 1999).

Bonobos have a more tolerant society. Whilst aggression and violence still occur, incidents are rarer and less severe (de Waal, 1995; Furuichi, 2011; Hare *et al.*, 2012). Instead, bonobos use socio-sexual behaviour to resolve conflicts (de Waal, 1995; Hare *et al.*, 2007; Stanford, 1998). Bonobo societies are matriarchal—an alpha female leads the group, and the oldest females are generally the highest ranked (de Waal, 1995; Furuichi, 2011). Male status is strongly influenced by their mother's status (Furuichi, 2011; Takeshi, 1997; de Waal, 1995). With mothers forming the core of bonobo society, the strongest bonds are between unrelated females and male-male bonds are weak (de Waal, 1995).

The subcomponents of the concept of death

The presence of the CoD in non-human animals is often contested due to a lack of a consistent definition (Gonçalves & Carvalho, 2019; Monsó & Osuna-Mascaró, 2020; Pettitt, 2018). Therefore, for my research into genus *Pan*, I was specifically looking for a human-like CoD, defined as an understanding that the body and mind have permanently ceased to function and that this state is an unpredictable phenomenon that eventually affects all living things (Kenyon, 2001). When studying the CoD in children, researchers assess understanding using the subcomponents of: 1) non-functionality (death entails the cessation of bodily and mental functions); 2) irreversibility (once an organism is dead, it cannot be returned to life); 3) universality (death happens to, and only to, living things); 4) inevitability (death happens to all living things); 5) personal mortality (death will happen to me); 6) causality (what causes death); and 7) unpredictability (that the timing of death cannot be known in advance) (Kenyon, 2001; Longbottom & Slaughter, 2018; Slaughter, 2005). Inevitability and mortality can be considered sub-aspects of universality (Speece & Brent, 1984, 1992), as the idea that death is universal to all living things inherently implies the inclusion of oneself and the exclusion of inanimate objects. Causality and unpredictability can be viewed as a step further than the fundamental CoD (Piaget, 1923), since to comprehend the causes of death and their unpredictability, an organism must already understand death as a basic concept.

Therefore, I collapsed inevitability and mortality into the universality component and excluded causality and unpredictability. I thus looked for evidence in genus *Pan* of just three subcomponents, defined as follows: non-functionality, being the understanding that death results in the complete cessation of bodily and mental functions; irreversibility, being the understanding that once an organism is dead, it cannot be returned to life; and universality, being the understanding that death also happens to all, and only, other living things—including oneself. In children, the acquisitional timing of the CoD can differ significantly, as the subcomponents are discrete and can develop in various orders (Speece & Brent, 1984, 1992). However, the most common developmental order is universality first, followed by non-functionality and irreversibility. Since the subcomponents are discrete, it is reasonable that some, but not all, may be present in *Pan*.

Research into the CoD in children relies on interviews and language development (Kenyon, 2001; Piaget, 1923). Non-functionality is considered acquired when variations of the question 'Can a dead thing do *x*?' are answered with 'No.' *X* may be any defining feature of life, from physical actions such as breathing or walking to invisible aspects such as thinking or feeling (Speece & Brent, 1984, 1992). Irreversibility is considered acquired when children answer 'No' to questions such as 'Can a dead person come back to life?', and answer the question '*How* can you make dead things come back to life?' with some variation of 'You cannot' (Piaget, 1923; Speece & Brent, 1984, 1992). Universality is considered acquired when children answer 'Yes' to questions regarding the death of other living things, such as 'Will *x* die one day?'—*x* may be the child, a person, an animal, or a plant (Piaget, 1923; Speece & Brent, 1984, 1992). That this previous research has relied on language is a significant obstacle when researching the CoD in non-human animals (Anderson, 2016), and I therefore needed to define non-linguistic behavioural equivalents.

Behavioural indicators of the concept of death

Non-linguistic behavioural indicators of non-functionality include treating the body in ways one would not if they were alive. *Pan* mothers often carry dead infants for extended periods after death (Biro *et al.*, 2010; Goldsborough *et al.*, 2020; Lonsdorf *et al.*, 2020; Watts, 2020). If they were to carry dead infants in atypical positions or treat them in a way that could have caused injury when alive, this indicates understanding of non-functionality. Cannibalism after death is a similar indicator, as no records exist of *Pan* cannibalising living conspecifics.

Deliberate checks for functionality also indicate understanding of non-functionality. These checks include actions that would have prompted responses if the deceased were merely sleeping, such as shaking or hitting the body, or checks for sensory cues of life, such as searching for breath or scent, as chimpanzees and bonobos rely more heavily on olfactory cues than humans (de Waal, 2019; van Leeuwen *et al.*, 2016). An organism's understanding of non-functionality must match its understanding of functionality, i.e., a chimpanzee cannot be expected to check for lack of brain activity, as they do not understand this to be a part of functionality.

Irreversibility can be seen via reactions to information received when searching for functionality. If, after inspecting a body, an individual then exhibits a strong emotional response (e.g., distress calls or physical agitation), this may indicate that they understand the deceased will never return to life. Stopping efforts to wake or revive the body after receiving no response also indicates an understanding that the state of death, unlike sleep, is irreversible. Burial or other deliberate disposal of the body indicates similar understanding.

Behavioural indicators of universality are harder to identify, as universality is less about an organism's immediate reaction to a death, which can be externally observed, and more about an internal transference of death's implications to future situations. Universality can be indicated if an organism reacts to heterospecifics differently once dead, as this demonstrates an understanding that non-functionality and irreversibility apply universally—not just to conspecifics. Universality can also be seen when grief and fear of death are transferred to other relationships (Speece & Brent, 1984, 1992), resulting in individuals who have experienced death taking extra care of remaining loved ones—including being overly protective of other children or exhibiting increased caution in situations that previously resulted in death.

To assess the extent of the CoD in *Pan*, I utilised these behavioural equivalents of the traditional subcomponents of the CoD for my guiding framework, as summarised in Table 1. I looked for recorded examples of these behaviours in chimpanzee and bonobo mortuary contexts. As I could not directly observe a community reacting to death, I was restricted to data from previous research. I collated various records of *Pan* mortuary behaviours from the existing published literature, both descriptions and videos of behaviour surrounding death. I obtained descriptions from primary research articles and preliminary reports, and videos from associated supplementary materials. Using solely anecdotal descriptions ran the risk of my research being influenced by others' biases; by utilising raw videos and making my own observations, I reduced possible bias and was able to notice behaviours that previous researchers had overlooked. Many of the videos were originally published for a different purpose—often the behaviours most relevant for my analysis occurred in the background and were not noted or discussed in the associated article. I systematically analysed these articles and videos with regard to my subcomponents, noting examples that fulfilled the requirements for the CoD.

Subcomponent	Verbal indicators in human children	Behavioural indicators in genus*Pan*
Non-functionality	Answering 'No' to a variation on 'Can a dead thing do *x*?'. *X* could be physical, like breathing or walking, or mental, like thinking or feeling (Speece & Brent, 1984, 1992).	Treating deceased bodies in ways they never would if alive; post-mortem cannibalism; deliberately checking for functionality and signs of life.
Irreversibility	Answering 'No' to questions such as 'Can a dead person come back to life?' and answering 'How can you make dead things come back to life?' with some variation of 'You cannot' (Piaget, 1923).	Stopping efforts to revive after receiving no response; strong emotional reactions to death; deliberate disposal of bodies.
Universality	Answering 'Yes' to questions regarding the death of other living things, such as 'Will *x* also die one day?'. *X* can be the child, another person, an animal, or a plant (Piaget, 1923; Speece & Brent, 1984, 1992).	Reacting to death in other species; showing increased caution and care for themselves or their loved ones.

Table 1: Summary of behavioural indicators of the concept of death in genus *Pan*

Chimpanzee and bonobo mortuary behaviours

Behaviours indicative of non-functionality

One behavioural indicator of non-functionality is treating bodies in a manner that one would not if they were alive. There are multiple instances of mothers carrying deceased infants in atypical positions. One female bonobo was recorded carrying her living infant ventrally; however, within hours of the infant's death, the mother began to carry the body dorsally and drag it along the ground (Fowler & Hohmann, 2010). Two chimpanzees with deceased infants transported them by gripping a limb and dragging or wedging the body between their neck and shoulder (Biro *et al.*, 2010). One mother also let juveniles drag the infant's body and play with it (Biro *et al.*, 2010). Other atypical carrying positions have included gripping the deceased infant in the mouth and slinging it over a shoulder or around the neck (Lonsdorf *et al.*, 2020; Watson & Matsuzawa, 2018). Post-mortem cannibalism, another example of treating dead bodies differently, also occurred after the bonobo infant's death: the alpha female led the group to feed on the body (Fowler & Hohmann, 2010). Other cases of post-mortem infant cannibalisation include a bonobo grooming and then eating her infant and a chimpanzee that partially cannibalised her infant before continuing to carry it for three days (Watson & Matsuzawa, 2018). Post-mortem cannibalism also occurred after a coalitionary attack on an adult male chimpanzee (Pruetz *et al.*, 2017).

Deliberately checking for functionality is also indicative of non-functionality, including checking for sensory cues that act as signs of life. A female chimpanzee inspected the bodies of a 9-year-old male and an infant by peering at the faces, sniffing the face and genitals, and touching the face and genitals before sniffing her hand (Cronin *et al.*, 2011; van Leeuwen *et al.*, 2016). Chimpanzees have also been recorded looking inside the mouths of deceased group members, including three chimpanzees prying open a closed mouth to inspect it thoroughly (Anderson *et al.*, 2010; de Waal, 2019).

Actions that would receive a response if the deceased were sleeping are another form of checking for functionality. These have been recorded in several forms: a male displayed over a body, hitting the ground with branches while vocalising (van Leeuwen *et al.*, 2016); after the previously mentioned coalitionary murder, a group member non-aggressively displayed, stamped, and pulled at the arms (Pruetz *et al.*, 2017); a young male lifted and shook the arm of a deceased group member then hit the torso when there was no response (Anderson *et al.*, 2010). Other groups have been recorded lifting limbs and dropping them (Biro *et al.*, 2010; de Waal, 2019). In all these cases, attempts to wake or revive the deceased stopped after receiving no response.

Behaviours indicative of irreversibility

Strong emotional responses after investigating the body of a conspecific, such as distress, are indicative of irreversibility. Cases of chimpanzees exhibiting distress after a death are numerous: one male made persistent 'wraaah' calls (a known sign of emotional distress), whimpered, watched the body for hours, and became agitated if others approached it (Teleki, 1973); a female who lost an infant refused to eat and rocked back and forth while screaming (de Waal, 2019); and, after a male failed to rouse a female he was bonded with, he screamed, tore at his hair, tried to prevent the body's removal, and spent days moaning and crying (Fiore, 2013). One of the most famous chimpanzee deaths is that of 8-year-old Flint (Fiore, 2013). After the death of his mother, Flo, whom he was unusually dependent on, he sank into a deep depression, eventually curling up and dying in the same spot where she died (Goodall, 1971). Some chimpanzee reactions to deaths of conspecifics are gentler, though still emotional: one female carefully groomed the bodies of a 9-year-old male and an infant for long after the rest of the group had lost interest, gently cleaning the male's teeth with a stem of grass (Cronin *et al.*, 2011; van Leeuwen *et al.*, 2016); after the death of her mother a female kept protective vigil over the body all night, while other females groomed it (de Waal, 2019); and, after the death of an older female, her close friend and daughter groomed the body and kept vigil through the night—they also refused to eat for weeks post-death and exhibited disturbed sleep (Anderson *et al.*, 2010).

Behaviours indicative of universality

Behavioural indications of universality can be found in individuals' reactions to the deaths of heterospecifics. When a chimpanzee group found a dying baboon, they became agitated and made persistent 'wraaah' calls (Teleki, 1973; van Lawick-Goodall, 1968). The chimpanzees sniffed, stroked, and groomed the body. The same group reacted with fear and avoidance when being presented with a live python but, upon seeing it killed, immediately reapproached the area, letting their infants touch the dead snake (van Lawick-Goodall, 1968). A similar reaction was recorded when a viper entered a bonobo sanctuary (de Waal, 2019). The group was initially afraid, but, after the alpha female killed the snake, juveniles playfully dragged the body and opened its mouth to inspect the fangs.

Another behaviour indicative of universality is changing one's behaviours towards others or oneself after experiencing death. I found no concrete examples of this, but there are two cases where unusual behaviours were exhibited. In the aforementioned case of Flo and Flint, Flint was unusually attached to his mother at such a late age due to her actions after her infant, Flame, died (Goodall, 1971). After Flame's death, Flo started babying 6-year-old Flint—carrying him on her back and sharing her food and night nest with him. In a different case, when a female chimpanzee carrying a recently deceased infant came across the body of a male group member, she swiftly moved away from the body to sit alone, clutching the body of her dead infant tighter to her chest (van Leeuwen *et al.*, 2016). However, there is also a potential counterexample where no change was shown when expected: after seeing a member of his group fall from a tree and break his neck, a chimpanzee almost fell from a tree in a similar manner when vines gave way beneath him (Teleki, 1973). He showed no extra caution when climbing, despite the death of his conspecific just hours earlier.

Discussion

Behavioural evidence for the concept of death in genus

There is abundant evidence for aspects of the CoD in *Pan*, specifically the non-functionality and irreversibility subcomponents. Both bonobos and chimpanzees demonstrated non-functionality by carrying deceased infants in atypical positions on six occasions and cannibalising bodies on four occasions. These atypical carrying positions—held in the mouth, wedged between the neck and shoulder, slung across the neck or shoulder, and dragged along the ground—were not seen when carrying sick, injured, or experimentally anesthetised infants (Lonsdorf *et al.*, 2020; Watson & Matsuzawa, 2018). This implies an understanding that death is a uniquely non-functional state. During cannibalism, only small pieces of flesh were eaten, implying that it was not for sustenance—a reasonable alternative hypothesis. Chimpanzees also demonstrated non-functionality via deliberate checks for functionality. They visually, physically, and olfactorily inspected faces, mouths, and genitals of dead conspecifics on six occasions; lifted and dropped limbs on three occasions; and displayed, vocalised at faces, and hit torsos on three occasions. The line blurs here between non-functionality and irreversibility—behavioural indicators of irreversibility include strong emotional responses after inspecting a body, which have been observed on at least ten occasions. However, it is difficult to differentiate between violence towards a body due to emotion and violence as an attempt to acquire information about the state of death. Nevertheless, even if these actions are not performed with the intention of investigating non-functionality, the faces and genitals that *Pan* attend to in life would be a rich source of information regarding the state of death (Cronin *et al.*, 2011).

Irreversibility is also demonstrated by stopping efforts to revive a body after receiving no response. In no case have displays, hitting, or vocalising continued for any significant period after failing to receive a response. Individuals that investigate bodies longest tend to be adolescents and juveniles, whereas those who have encountered death before, such as older group members (Cronin *et al.* 2011; van Leeuwen *et al.*, 2016), investigate bodies for shorter amounts of time. This suggests that the CoD in *Pan* is learnt rather than innate—the implication being that the *Pan* CoD is closer in nature to the human CoD, which is learnt through experience and teaching (Kenyon, 2001; Speece & Brent, 1984, 1992), than the partial CoD of species such as ants, which is instinctual and automatic (Fashing & Nguyen, 2011; Monsó & Osuna-Mascaró, 2020). There are no recorded cases of burial or deliberate disposal of bodies, which would have been a third indicator of irreversibility. One behavioural indicator that I did not anticipate when creating my framework, but encountered during analysis, was expressions of alarm when dead bodies act in a way expected only of the living. In the coalitionary killing (Pruetz *et al.*, 2017), researchers buried the corpse after the group moved away. Upon returning to the area and finding the body gone, the group made frequent, nervous alarm calls—as if they feared the absence of the body. Their fear indicates an understanding that the dead cannot independently move position or location, and that this non-functionality is irreversible, with no return to movement to be expected. This emphasises that the troop construed the deceased's lack of responsiveness as a permanent, rather than temporary, state.

The cases of post-mortem cannibalism (Fowler & Hohmann, 2010; Pruetz et al., 2017; Watson & Matsuzawa, 2018) also demonstrate irreversibility. These behaviours suggest an understanding of the permanent nature of death, as no cases of ante-mortem cannibalism have been recorded in genus *Pan*—even in cases of long-term unresponsiveness and loss of consciousness. This strengthens the case for a CoD, as these actions cannot be explained as simply responses to the unexpected cessation of movement, but are reactions that make sense if, and only if, the individual construes the situation as permanent and irreversible.

The final subcomponent, universality, has not been satisfactorily demonstrated. Behavioural universality indicators include exhibiting understanding that non-functionality and irreversibility apply equally to heterospecifics and conspecifics. There is one case each for chimpanzees and bonobos where their fearful reactions to a snake changed once it died and was no longer a threat, and there is a single case of chimpanzees reacting with distress to the death of a baboon. The baboon incident is notable since baboons are common prey for chimpanzees, so their death should not logically be distressing. It is possible that upon encountering the dying baboon outside of a predatory context, the chimpanzees were reminded of the deaths of conspecifics—if so, this would be a case of universality. The second group of behaviours indicative of universality, including taking extra care of loved ones or oneself after a death, has only two possible examples, both in chimpanzees, and one possible counterexample. However, the counterexample, where the chimpanzee demonstrated no increase in caution after a conspecific fell to his death, may not be what it seemed. The human observers did not directly observe the moment when the deceased fell—they were alerted to the incident by his landing and inferred what must have occurred. The other chimpanzee may have been in a similar situation, where he did not observe the exact moment or manner of death.

Overall, it is reasonable to conclude that genus *Pan* possesses the CoD. However, it appears to fall short of the level of CoD seen in modern humans, with only non-functionality and irreversibility satisfactorily demonstrated. This is unexpected, as universality is the first of the three subcomponents to develop in children (Kenyon, 2001). It is possible that universality may be present in *Pan* and simply absent from this data due to its nature being extremely difficult to perceive via behaviour alone.

The social and emotional origins of the Pan *concept of death*

In human children, the extent of the exhibited CoD varies according to the strength of the child's relationship with the deceased (Speece & Brent, 1984, 1992). A similar phenomenon appeared in this research, as the individuals most affected by each death were those emotionally closest to the deceased. In the falling death, the individual who made 'wraaah' calls, whimpered, and became agitated if others approached the body was a close friend of the deceased (Teleki, 1973). In the coalitionary murder, the group member who displayed, vocalised, pulled at the body, and refused to participate in cannibalism, was one of only two individuals who had previously engaged in affiliative behaviour with the deceased (Pruetz *et al.*, 2017). The 9-year-old who died of illness was a highly social individual who roamed between subgroups—accordingly, most of the group was interested in and protective of the body (van Leeuwen *et al.*, 2016). Even then, the two most affected were his closest male friend, who displayed over the body, forced access to it, and visited more than any other male, and his adopted aunt, who groomed the body, cleaned his teeth, and kept vigil once others had left.

Conversely, after the death of a female chimpanzee who was low-ranked and socially peripheral, the only group member to spend significant time near the body, and the only female to handle the body at all, was her daughter (Stewart *et al.*, 2012). Infants are also socially peripheral, not yet having formed relationships outside of their mother—unsurprisingly, in cases of infant death, only the mothers had noticeable emotional responses to the death (Biro *et al.*, 2010; Cronin *et al.*, 2011; de Waal, 2019). Overall, individuals' reactions to death vary by the closeness of their living relationship to the deceased. Mortuary behaviours in *Pan* are a translation of the bonds created in life.

The *Pan* CoD also appears to be more of an emotional reaction than categorisable behaviour. Several cases blur the lines between subcomponents, but the common factor is that group members are distressed, upset, or unsettled. Frans de Waal (2019) coined the term *anthropodenial* for when researchers reject similarities between humans and our close relatives to keep humans on an evolutionary pedestal. Many scholars criticise anthropomorphism (Gruber & Clay, 2016), but I believe anthropodenial is worse. If two closely related taxa act similarly under similar circumstances, then it is reasonable to believe they are similarly driven. Therefore, I describe this emotional response to death as grief, and the behaviours that stem from it, such as grooming and keeping vigil, as mourning. In humans, grief is a feeling of sorrow caused by distress over a loss (Fiore, 2013; Gonçalves & Carvalho, 2019), with mourning then being the suite of social behaviours exhibited in response to that grief (Gonçalves & Carvalho, 2019). As the *Pan* CoD appears rooted in grief and mourning, it is reasonable to call it an emotionally and socially driven phenomenon.

As I am looking at a human-like CoD from an evolutionary perspective, the next step is to theorise the evolutionary function of a socially and emotionally driven CoD. I believe it most likely evolved as a social adaptation. Death impacts society by severing social bonds and thus creates a rupture in the social fabric: the most social animals have the most mourners as they had numerous strong bonds in life. The CoD evolved because it is needed as a social stabiliser. If a species develops the ability to understand death, they can feel grief. If a species can feel grief, then they can begin to mourn. If a species can mourn, they can more quickly recategorise the living to dead, reform the social structure, and shape a new dominance network after death has left a hole in the hierarchy. A human-like CoD would therefore be an adaptation to protect against destabilisations caused by death. The more social and communal a species, the more effort must be put into protecting against social destabilisation—thus a human-like CoD is more likely to evolve. Chimpanzees and bonobos, like humans, are highly social animals to whom a defined hierarchy is vital for stability. If *Pan* indeed has the human-like CoD that they appear to have in this research, and if that CoD evolved for the reasons hypothesised, then it is reasonable to say that our early hominin ancestors most likely possessed such a CoD too.

Conclusion and directions for further research

Genus *Pan* has a complex CoD, including a cogent understanding of the biological subcomponents of non-functionality and irreversibility and at least some degree of understanding of the more metaphysical subcomponent of universality. They may, however, understand more of universality than it appears, as behaviour struggles to accurately reveal emotion—and emotion appears to be the main driver of the *Pan* CoD. That is the principal limitation of this work. However, if a human-like CoD is indeed a social adaptation to sustain complex hierarchies and protect large group sizes against destabilisation, then it is reasonable to conclude that both *Pan* and early hominins had a significant understanding of death.

There are some avenues of future research that may bring us closer to a definite answer. One behaviour that should be watched for is whether, after losing an infant, a mother treats her future infants with increased care and is more protective and watchful. If so, then this would indicate a more robust understanding of universality. We can also watch for the effects of social destabilisation in other parallel settings that do not invoke grief. Suppose grief and mourning are, in fact, adaptations for stability. In that case, one might expect to see the hierarchy restabilise slower if individuals were removed from the group in ways other than death, such as peaceful emigrations from the natal group or transfers to other zoos or sanctuaries. One pitfall that future researchers need to be wary of is preconceived notions of the “correct” reaction an individual should have to death. Harris (2018), for example, proposes an experiment where vocal recordings of deceased individuals are played to a chimpanzee troop. Harris theorises that, if the troop truly understood the irreversibility of the death state, then they should exhibit consternation and fear upon hearing the voice of their dead conspecific, and not excitement or relief at their supposed return. Putting aside the unethical nature of deliberately subjecting individuals to potential distress, this proposal is founded in a belief that the “correct” reaction to apparent resurrection should be negative, when, even within *Homo sapiens*, various historical and extant religions have believed that resurrection is both possible and positive (Habermas, 1989; Lehtipuu, 2015). Future work also needs to focus more heavily on bonobos, as bonobo reactions to death are largely missing from the literature. This means that we have been defining a genus by the behaviour of one species, which may be skewing the findings (Gruber & Clay, 2016). There is copious research potential in this still-developing field of evolutionary primate thanatology.

Acknowledgments

I have immense gratitude for the expert guidance of Prof. Judith Littleton and Dr Nicholas Malone, without whom this research would have never even begun. Thank you for giving up your summers for me.

List of tables

References

Anderson, J. R. (2016), ‘Comparative thanatology’, *Current Biology*, 26 (13), R553–56, https://doi.org/10.1016/j.cub.2015.11.010

Anderson, J. R., Biro, D., and P. Pettitt (2018), ‘Evolutionary thanatology’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373 (1754), https://doi.org/10.1098/rstb.2017.0262

Anderson, J. R., Gillies, A., and L. C. Lock, (2010) ‘Pan thanatology’, *Current Biology,* 20 (8), R349–51, https://doi.org/10.1016/j.cub.2010.02.010

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Di Fiore, A., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernandez, G., Strier, K. B., and C. P. van Schaik (2008), ‘Fission-fusion dynamics: New research frameworks’, *Current Anthropology*, 49 (4), 627–54, https://doi.org/10.1086/586708

Biro, D., Humle, T., Koops, K., Sousa, C., Hayashi, M., and T. Matsuzawa (2010), ‘Chimpanzee mothers at Bossou, Guinea carry the mummified remains of their dead infants’, *Current Biology*, 20 (8), R351–52, https://doi.org/10.1016/j.cub.2010.02.031

Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y., and E. Normand (2008), ‘Intergroup conflicts among chimpanzees in Taï National Park: Lethal violence and the female perspective’, *American Journal of Primatology*, 70 (6), 519–32, https://doi.org/10.1002/ajp.20524

Cronin, K. A., van Leeuwen, Edwin J. C., Mulenga, I. C., and M. D. Bodamer (2011), ‘Behavioral response of a chimpanzee mother toward her dead infant’, *American Journal of Primatology,* 73 (5), 415–21, https://doi.org/10.1002/ajp.20927

de Waal, F. (1995), ‘Bonobo sex and society’, *Scientific American*, 272 (3), 82–88, https://www.jstor.org/stable/24980375

de Waal, F. (2019), *Mama’s Last Hug*, London: Granta (originally published by W. W. Norton & Company)

Doran, D. M. (1993), ‘Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion’, *American Journal of Physical Anthropology*, 91 (1), 83–98, https://doi.org/10.1002/ajpa.1330910106

Dunbar, R. I. M. and S. Shultz (2007), ‘Evolution in the social brain’, *Science*, 317 (5843), 1344–47, https://doi.org/10.1126/science.1145463

Fashing, P. J. and N. Nguyen (2011), ‘Behavior toward the dying, diseased, or disabled among animals and its relevance to paleopathology’, *International Journal of Paleopathology*, 1 (3-4), 128–29, https://doi.org/10.1016/j.ijpp.2012.02.004

Fiore, R. R. (2013), ‘What defines us: An analysis of grieving behavior in non-human primates as a potential evolutionary adaptation’, unpublished undergraduate Honors thesis, University of Colorado at Boulder, https://scholar.colorado.edu/concern/undergraduate_honors_theses/70795803j

Foerster, S., Franz, M., Murray, C. M., Gilby, I. C., Feldblum, J. T., Walker, K. K., and A. E. Pusey (2016), ‘Chimpanzee females queue but males compete for social status’, *Scientific Reports,* 6 (35404), 1–11, https://doi.org/10.1038/srep35404

Fowler, A. and G. Hohmann (2010), ‘Cannibalism in wild bonobos (*Pan paniscus*) at Lui Kotale’, *American Journal of Primatology*, 72 (6), 509–14, https://doi.org/10.1002/ajp.20802

Furuichi, T. (2011), ‘Female contributions to the peaceful nature of bonobo society’, *Evolutionary Anthropology*, 20 (4), 131–42, https://doi.org/10.1002/evan.20308

Goldsborough, Z., van Leeuwen, E. J. C., Kolff, K. W. T., de Waal, F. B. M., and C. E. Webb (2020), ‘Do chimpanzees (*Pan troglodytes*) console a bereaved mother?’, *Primates*, 61, 93–102, https://doi.org/10.1007/s10329-019-00752-x

Gonçalves, A. and D. Biro (2018), ‘Comparative thanatology, an integrative approach: Exploring sensory/cognitive aspects of death recognition in vertebrates and invertebrates’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373 (1754), https://doi.org/10.1098/rstb.2017.0263

Gonçalves, A. and S. Carvalho (2019), ‘Death among primates: A critical review of non-human primate interactions towards their dead and dying’, *Biological Reviews*, 94 (4), 1502–29, https://doi.org/10.1111/brv.12512

Goodall, J. (1971), *In the Shadow of Man*, Boston: Mariner Books.

Gruber, T. and Z. Clay. (2016), ‘A comparison between bonobos and chimpanzees: A review and update’, *Evolutionary Anthropology*, 25 (5), 239–52, https://doi.org/10.1002/evan.21501

Habermas, G. (1989), ‘Resurrection claims in non-Christian religions’, *Religious Studies*, 25 (2), 167–177, https://doi.org/10.1017/S0034412500001785

Hare, B., Melis, A. P., Woods, V., Hastings, S., and R. Wrangham (2007), ‘Tolerance allows bonobos to outperform chimpanzees on a cooperative task’, *Current Biology*, 17 (7), 619–23, https://doi.org/10.1016/j.cub.2007.02.040

Hare, B., Wobber, V., and R. Wrangham (2012), ‘The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression’, *Animal Behaviour*, 83 (3), 573–85, https://doi.org/10.1016/j.anbehav.2011.12.007

Harris, P. L. (2018), ‘Children’s understanding of death: From biology to religion’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373 (1754), https://doi.org/10.1098/rstb.2017.0266

Kenyon, B. L. (2001), ‘Current research in children’s conceptions of death: A critical review’, *OMEGA*, 43 (1), 63–91, https://doi.org/10.2190/0X2B-B1N9-A579-DVK1

Lehtipuu, O. (2015), *Debates Over the Resurrection of the Dead: Constructing Early Christian Identity*, Oxford: Oxford University Press.

Longbottom, S. and V. Slaughter (2018), ‘Sources of children’s knowledge about death and dying’, *Philosophical Transactions of the Royal Society B: Biological Sciences,* 373 (1754), 20170267, https://doi.org/10.1098/rstb.2017.0267

Lonsdorf, E. V., Wilson, M. L., Boehm, E., Delaney-Soesman, J., Grebey, T., Murray, C., Wellens, K., and A. E. Pusey (2020), 'Why chimpanzees carry dead infants: An empirical assessment of existing hypotheses', *Royal Society Open Science*, 7 (7), https://doi.org/10.1098/rsos.200931

Monsó, S. and A. J. Osuna-Mascaró (2020), 'Death is common, so is understanding it: The concept of death in other species', *Synthese,* 1–25, https://doi.org/10.1007/s11229-020-02882-y

Piaget, J. (1923), *Le langage et la pensée chez l'enfant: Études sur la logique de l'enfant*, (9th ed.), Paris: Delachaux et Niestlé

Pepper, J. W., Mitani, J. C., and D. P. Watts (1999), 'General gregariousness and specific social preferences among wild chimpanzees', *International Journal of Primatology*, 20 (5), 613–32, https://doi.org/10.1023/A:1020760616641

Pettitt, P. (2018), 'Hominin evolutionary thanatology from the mortuary to funerary realm: The palaeoanthropological bridge between chemistry and culture', *Philosophical Transactions of the Royal Society B: Biological Sciences,* 373 (1754), 20180212, https://doi.org/10.1098/rstb.2018.0212

Pruetz, J. D., Ontl, K. B., Cleaveland, E., Lindshield, S., Marshack, J., and E. G. Wessling, (2017), 'Intragroup lethal aggression in West African chimpanzees (*Pan troglodytes verus*): Inferred killing of a former alpha male at Fongoli, Senegal', *International Journal of Primatology*, 38, 31–57, https://doi.org/10.1007/s10764-016-9942-9

Slaughter, V. (2005), 'Young children's understanding of death', *Australian Psychologist*, 40 (3), 179–86, https://doi.org/10.1080/00050060500243426

Sobolewski, M. E., Brown, J. L., and J. C. Mitani (2012), 'Territoriality, tolerance and testosterone in wild chimpanzees', *Animal Behaviour*, 84 (6), 1469–74, https://doi.org/10.1016/j.anbehav.2012.09.018

Speece, M. W. and S. B. Brent (1984), 'Children's understanding of death: A review of three components of a death concept', *Child Development*, 55 (5), 1671–86, https://doi.org/10.2307/1129915

Speece, M. W. and S. B. Brent (1992), 'The acquisition of a mature understanding of three components of the concept of death', *Death Studies*, 16 (3), 211–29, https://doi.org/10.1080/07481189208252571

Stanford, C. B. (1998), 'The social behavior of chimpanzees and bonobos: Empirical evidence and shifting assumptions', *Current Anthropology*, 39 (4), 399–420, https://doi.org/10.1086/204757

Stewart, F. A., Piel, A. K., and R. C. O'Malley (2012), 'Responses of chimpanzees to a recently dead community member at Gombe National Park, Tanzania', *American Journal of Primatology,* 74 (1), 1–7, https://doi.org/10.1002/ajp.20994

Suddendorf, T. (2004), 'How primatology can inform us about the evolution of the human mind', *Australian Psychologist*, 39 (3), 180–87, https://doi.org/10.1080/00050060412331295117

Takeshi, F. (1997), 'Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba', *International Journal of Primatology*, 18 (6), 855–75, https://doi.org/10.1023/A:1026327627943

Teleki, G. (1973), 'Group response to the accidental death of a chimpanzee in Gombe National Park, Tanzania', *Folia Primatologica*, 20, 81–94, https://doi.org/10.1159/000155569 van Lawick-Goodall, J. (1968), 'The behaviour of free-living chimpanzees in the Gombe Stream Reserve', *Animal Behaviour Monographs,* 1 (Pt. 3), 161–311, IN1–12, https://doi.org/10.1016/S0066-1856(68)80003-2

van Leeuwen, E. J. C., Mulenga, I. C., Bodamer, M. D., & Cronin, K. A. (2016). Chimpanzees' responses to the dead bodyhttps://doi.org/10.1002/ajp.22560 of a 9-year-old group member. *American Journal of Primatology, 78*(9), 914–22,

Watson, C. F. I., & Matsuzawa, T. (2018). Behaviour of non-human primate mothers toward their dead infants: uncovering mechanisms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1754), https://doi.org/10.1098/rstb.2017.0261

Watts, D. P. (2020). Responses to dead and dying conspecifics and heterospecifics by wild mountain gorillas (*Gorilla beringei beringei*) and chimpanzees (*Pan troglodytes schweinfurthii*). *Primates*, *61*, 55–68, https://doi.org/10.1007/s10329-019-00735-y

Glossary

Affiliative behaviour: a behaviour or activity that builds unity within a group or bondedness between a pair.

Conspecific: an organism belonging to the same species.

Dominance display: behaviours designed to reinforce dominance over other individuals such as vocalising, beating the chest, or waving branches.

Genus *Homo*: the biological group that includes modern *Homo sapiens* (humans) and our closest extinct relatives.

Genus *Pan*: the biological group that includes the chimpanzee and bonobo but excludes other great apes, e.g., humans or gorillas.

Heterospecific: an organism belonging to a different species.

Hominin: the biological group that includes all modern and extinct humans and our ancestors, but excludes genus *Pan*.

Natal group: the group that an individual was born into, as opposed to one they join later in life via mating.

Taxa: any unit of biological classification, e.g., species, genus, family, order.

Thanatology: the scientific study of death.

To cite this paper please use the following details: McLean, K. H. (2024), 'A Concept of Death in Genus Pan: Implications for Human Evolution', *Reinvention: an International Journal of Undergraduate Research*, Volume 17, Issue 1, https://reinventionjournal.org/article/view/1258. Date accessed [insert date]. If you cite this article or use it in any teaching or other related activities please let us know by e-mailing us at Reinventionjournal@warwick.ac.uk.

https://doi.org/10.31273/reinvention.v17i1.1258, ISSN 1755-7429, c 2024, contact, reinventionjournal@warwick.ac.uk
Published by University of Warwick and Monash University, supported by the Monash Warwick Alliance.