PHILOSOPHICAL TRANSACTIONS B

rstb.royalsocietypublishing.org

Opinion piece

Cite this article: Anderson JR. 2018 Chimpanzees and death. *Phil. Trans. R. Soc. B* **373**: 20170257.
http://dx.doi.org/10.1098/rstb.2017.0257

Accepted: 20 May 2018

One contribution of 18 to a theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

Subject Areas:
behaviour, cognition

Keywords:
chimpanzees, dying, death, predation, aggression, suicide, culture

Author for correspondence:
James R. Anderson
e-mail: j.r.anderson@psy.bun.kyoto-u.ac.jp

Chimpanzees and death

James R. Anderson

Department of Psychology, Graduate School of Letters, Kyoto University, Kyoto 606-8501, Japan

JRA, 0000-0003-2441-0728

Information about responses to death in nonhuman primates is important for evolutionary thanatology. This paper reviews the major causes of death in chimpanzees, and how these apes respond to cues related to dying and death. Topics covered include disease, human activities, predation, accidents and intra-species aggression and cannibalism. Chimpanzees also kill and sometimes eat other species. It is argued that, given their cognitive abilities, their experiences of death in conspecifics and other species are likely to equip chimpanzees with an understanding of death as cessation of function and irreversible. Whether they might understand that death is inevitable—including their own death, and biological causes of death is also discussed. As well as gathering more fundamental information about responses to dying and death, researchers should pay attention to possible cultural variations in how great apes deal with death.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

1. Introduction

Given favourable social and environmental conditions—such as abundant food, few predators, absence of epidemics and little disturbance from humans—chimpanzees might live until at least 50 years of age. However, as a result of various challenges to their survival at different stages of life most chimpanzees do not live as long, and males generally die earlier than females [1–4]. At Mahale (Tanzania), around half of all infant chimpanzees die before they are weaned [5].

Deaths have been witnessed or inferred by researchers at all long-term chimpanzee study sites. Because female chimpanzees tend to emigrate from their natal communities, unexplained disappearances are conservatively assumed to reflect possible transfer. By contrast, if infants, juveniles or adult males disappear researchers often consider them to have died, although this often goes unverified. Even when dead chimpanzees are found it is not always possible to establish the precise cause of death [6–9]. Known and inferred mortality factors in wild chimpanzees include disease, hunting by humans, nonhuman predators, general senescence, accidents and intra- and inter-group aggression [3,4]; some factors reported in captivity [10] are also likely to apply to wild populations. The aims of this paper are to (1) review causes of death in chimpanzees, (2) consider how chimpanzees respond to death and death-related cues and (3) address the question how chimpanzees' 'psychology of death' compares with that of their nearest evolutionary neighbours, namely humans. The broader, overall aim is to stimulate primatologists to gather and present further information to help progress in the field of comparative evolutionary thanatology.

2. Causes of death

(a) Disease

Chimpanzees in the wild are susceptible to a range of potentially fatal diseases such as pneumonia, human respiratory viruses, simian immunodeficiency viruses, Ebola and anthrax [11–16]. Diseases accounted for most deaths of

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known cause in the early years of research at Gombe (Tanzania) [11,17,18]. Cross-infection may occur from humans (researchers, park employees, local people, tourists) to chimpanzees [14,19]. Following the establishment of improved prevention protocols for humans at Gombe, respiratory disease-related deaths in chimpanzees declined sharply [9]. Some diseases might cause death indirectly; for example, severely weakened individuals may be more prone to accidents or more vulnerable to predatory attacks. Chimpanzees naturally infected with *Toxoplasma* have been found to show abnormal levels of interest in leopard urine, which would likely be maladaptive under normal circumstances [20].

(b) Humans

In many areas where they live chimpanzees are deliberately killed by humans for meat, for body parts in traditional medicine (or as charms), or to obtain infants as pets or to sell. It is estimated that 5–10 chimpanzees are killed for every infant captured alive [21]. Poaching poses a serious threat to many populations, especially in areas where armed conflicts result in food shortages and a breakdown of law and order, and when mining or timber-felling operations open up new roads that facilitate access to forests [22,23]. Chimpanzees are also killed in retaliation for crop raiding or aggression toward humans [8,24–26].

The replacement of traditional weapons (e.g. spears, bows and arrows) by guns has made it easier to kill chimpanzees and other wildlife. Snares and mantraps are sometimes set specifically for chimpanzees, although they are generally more often used to capture other animals [27,28]. Many chimpanzees lose fingers, toes, hands or feet after getting caught in snares, and some survivors have wire embedded in their flesh for a long time [29–31]; death from infection must befall some injured victims [28,32,33]. Snare-injured chimpanzees in Budongo (Uganda) carry higher helminth parasite loads than non-injured controls, indicating secondary and/or long-term effects on health [34].

Another anthropogenic cause of deaths in chimpanzees is motor vehicles [35]. A recent report described the case of an adult female in Uganda killed by a fast-moving taxi as she tried to cross a road [36]. The mortality risk to chimpanzees from vehicular traffic seems bound to increase with the massive expansion of road building and vehicles travelling at greater speeds [37].

(c) Nonhuman predators and other species

Lions and leopards are known predators of chimpanzees [38–41], although in the absence of direct evidence scavenging cannot always be ruled out [42]. One or more leopards was the primary cause of chimpanzee mortality during a 5-year period in the Taï Forest (Ivory Coast) [43], and at least eight individuals at Mahale were presumed killed by lions over a 2-year period [40]. Among other potential predators, hyenas and African hunting dogs [44,45] are probably of little threat to healthy adult chimpanzees owing to the latters' strength and agility, but capable of finishing off sick or injured individuals.

Despite no records of chimpanzees being eaten by pythons, these snakes are also considered as potential predators [46]. Similarly, given that they consumed early hominids and kill modern humans [47], crocodiles in and around rivers and water holes should be considered as potential predators [48]. Finally, although venomous snakes such as cobras and vipers do not prey on chimpanzees, their bites could be fatal; researchers frequently encountered these species in the savannah-woodland habitat of chimpanzees at Mount Assirik (Senegal) [49].

(d) Accidents

Falling out of trees presents a real danger to large-bodied primates, as indicated by direct observations of the fall-related injuries and post-mortem signs of bone damage [8,9,50,51]. It has been even been argued that fractures on the skeleton of the australopithecine 'Lucy' indicate death from a fall [52]. Fatal falls represented 10% of the sample in a study of Kibale chimpanzee corpses [8]. Gombe adults were most likely to fall during fights [11], and all falls witnessed during a 17-year period at Taï were fight-related [30]. An aggression-related fatal fall was recently reported in a zoo-housed chimpanzee group [53].

One fatal fall at Gombe was by an adult male who died instantly from a broken neck when he hit the ground after the branch supporting him broke [54]; another was by an infant who got blown out of a tree by a gust of wind and who died from suspected internal injuries a few days later [11]. Usually when youngsters fell it was during play and resulted in fewer injuries than in adults, who fell from greater heights [11]. The death of one Taï infant was attributed to a fall [30]. Post-mortem examination of an adult female at Mahale revealed six fractured ribs, suggesting haemorrhagic shock and death shortly after a fall [55]. Researchers at Mahale also reported an unusual but fatal arboreal accident. An abandoned dead infant was found jammed between two overlapping tree boughs. Death was attributed to one bough springing back after being displaced by a heavier, stronger individual—most likely the mother—and crushing the infant [56].

Chimpanzees are not good swimmers, and several deaths by drowning have been reported. Although no reports concern fully wild chimpanzees, some captives released onto an island drowned [57], probably after wading too far into the water. Several zoo-housed chimpanzees have drowned after jumping or falling into moats [58–60].

(e) Conspecifics

Numerous killings of chimpanzees by other chimpanzees have been observed, and further cases have been inferred from wounds on fresh corpses or results of post-mortems [61]. Conspecific killing was the most important cause of death at Gombe between August 2004 and January 2010 [9]. Over a 50-year period at Mahale at least 29 chimpanzees were possible victims of lethal aggression by conspecifics, although when stricter criteria are applied the number drops to 12 [62]. In all 12 cases both attackers and victims were male, a sex bias that emerged also in a multi-site study of 152 intraspecific killings (males accounting for 92% of attackers and 73% of victims) [61].

Intraspecific killing includes infanticide—typically by adults—as well as fatal attacks on adults by other adults [11,61,63]. Whereas a single adult can quite easily kill an infant, it takes a sustained onslaught by several individuals to kill an adult [64]. At Gombe inter-group killings eventually resulted in the elimination of an entire neighbouring community [11], and by wiping out most of their neighbours over a

10-year period a chimpanzee community at Ngogo (Kibale) significantly expanded its home range [65]. In keeping with a direct competition/territorial expansion hypothesis, most victims in 152 observed, inferred or suspected intraspecific killings at five study sites across Africa were members of other communities [61]. Within-group killings of adults have also been reported, both in captivity and in the wild [66–71].

3. Responses to dead animals

(a) Conspecifics: non-cannibalistic responses

Reports about how captive and free-living chimpanzees respond to dead conspecifics vary in details about circumstances of the death and the behaviours shown. The well-known phenomenon of mothers continuing to transport and care for dead infants (and others' reactions) have been well documented elsewhere [72–74]. Here, other categories are considered. Two early accounts are notable for the contrasting responses of young captive chimpanzees to the death of their cagemate. One youngster was found sitting silently and subdued beside his dead companion, who was covered by a blanket. When the body was removed the youngster became agitated, but after being released from his cage he reportedly calmed down and watched as the corpse was dissected [75]. Another youngster vocalized loudly and threw a temper tantrum when his companion died, vigorously pulling, pushing and lifting up the head and hands; he remained agitated for the rest of the day after the body was removed [76]. In both of these cases the survivor may have been frightened by the dramatic change in the companion, from active and interactive to inert and unresponsive.

Fright and heightened arousal characterized Gombe chimpanzees' reactions to the sudden death of an adult male who fell out of a tree [54]. The ensuing general frenzy included loud vocalizations and displays, and mutual embracing, as well as frequent visual and olfactory inspection of the corpse. Gradually, the chimpanzees calmed down and engaged in quiet social activities; several individuals approached and peered at the corpse, but none physically contacted it in the several hours before it was finally abandoned.

Outbursts of vocalizations and aggressive displays interspersed with periods of silence were also recorded at Taï when a leopard killed an adolescent female. By contrast to the post-accident scene at Gombe, however, the Taï chimpanzees frequently touched the dead female, including grooming, and holding and gently pulling her hand; adult males even dragged the corpse along the ground for several metres [30]. Adult males also prevented some individuals from approaching the corpse, notably infants and a low-ranking female. On discovering another (adult) female's body with no obvious signs of injury, Taï chimpanzees sporadically alarm called, screamed and pant-hooted during the 5 h that they remained nearby. They mostly looked down at the corpse from overhead branches, but a few descended to the ground and touched it, one male doing do aggressively [33].

At Gombe, the corpse of an adult female who died after being visibly sick for several days received aggressive treatment from some of the 16–18 individuals present [77]. This account is especially notable for the bouts of rough handling and dragging of the body by young males; other members of the party did little more than look at, sniff or groom the body. Among several females present, only the dead female's daughter physically contacted the body.

The possible influence of the pre-death social relationship with the dead individual on post-death responses is illustrated by a recent case involving a dead 9-year-old male. After discovering the corpse, members of a sanctuary-housed group of chimpanzees sat quietly nearby for most of a 20 min period during which the scene was video recorded [78]. Many individuals looked closely at and sometimes clustered around the body, with at least nine physically contacting it. Two individuals—an adult male and an adult female—were briefly aggressive; the adult female slapped the body. One male who showed special interest had been the closest companion of the dead individual after the latter's mother died 3 years earlier. Towards the end of the observation period an adult female closely inspected the corpse and cleaned the teeth with a grass stem, which she occasionally also put in her own mouth.

(b) Conspecifics: cannibalism

Not only are some chimpanzees killed by conspecifics, they also get cannibalized: the killers and sometimes bystanders eat parts of the dead body [11]. Most reports concern infants of 'stranger' females getting killed and eaten, but intra-group cases also occur [79]. The rate of post-infanticide cannibalism is higher in chimpanzees than other species of nonhuman primates [80]; a review of 40 cases revealed that 23% of chimpanzee infanticide victims were consumed wholly, and another 37.5% partially [81].

More rarely, adults may also be cannibalized, as happened following the killing of a former dominant male at Fongoli (Senegal). Several of the victim's attackers and others abused the corpse, and several individuals ate parts of it; one adult female in particular tore pieces off the body with her teeth and ate them [71]. Following a lethal gang attack on a lone male from another group in the Taï forest, a participating adult female reportedly ate the victim's severed genitals [39].

(c) Non-conspecifics

Chimpanzees occasionally eat parts of dead animals that they have not themselves killed, but scavenging is generally uncommon. The predominant response towards discovered non-conspecific corpses is short-lived curiosity [74,82–85]. However, Gombe chimpanzees reacted with fear-related 'wraaah' calls when they encountered a recently killed adult bushpig; several individuals sniffed the surrounding ground and vegetation, in what van Lawick-Goodall [74] suggested might be an attempt to get olfactory information about the cause of death (the bushpig was killed by humans).

4. Responses to danger and death-related contexts

The above overview sets the scene for examining how chimpanzees behave when confronted with cues that are related to death and dying. Such cues include dead individuals (discussed above), sick individuals and potentially dangerous situations such as being high up in a tree, near a territorial

boundary or in proximity to humans or predators. Consideration of these aspects paves the way for discussion of what chimpanzees might understand and feel about death.

(a) Diseased conspecifics

An individual stricken with a potentially fatal contagious disease presents a risk to its companions. Do chimpanzees show evidence of awareness of this? Little is known about responses to visibly ailing or dying conspecifics in the wild [86]; overall reactions have been described as 'ambivalent' [16]. Reported responses include adults attacking newly partially paralysed victims of polio [74], slowing down to allow an old, sick female to keep up [87], tending and sharing food with a sick, injured old relative [11] and mothers giving extra support to sick infants that cannot cling normally, or re-settling them if they shows signs of discomfort [11,74,88]. Non-relatives showed no negative reactions to a disabled infant [88]. Empathic responses towards sick and dying companions have also been described in captivity [89–91].

Injured chimpanzees, for example those bearing wounds resulting from intra-group fighting, may receive 'comforting' attention and grooming from companions [40]. At Gombe kin or close friends in particular tended others' wounds [11], whereas at Taï wounded chimpanzees—including those injured by leopards—also received care from non-relatives [33]. With the exception of the reported attacks on polio victims at Gombe, chimpanzees in the wild do not appear to discriminate against or shun sick or injured companions.

(b) Humans

Unhabituated wild chimpanzees usually flee when they first encounter researchers [92,93]. Habituation may take months or years, but groups with less negative exposure to humans may show less avoidance, and some may appear relaxed or even intimidate human intruders [94–96]. Chimpanzees high up in trees, males, and those in large parties are less skittish than those on the ground, females, or those in small parties [95,97]. Occasionally, chimpanzees living near humans have attacked them, usually in response to provocation or harassment [98]. Previous experience and current context likely combine to determine responses to humans, eliciting a range of anti-predator-like behaviours in at least some populations [99].

Responses on discovering snares indicate recognition of potential danger. At Bossou (Guinea), when chimpanzees discover snares they try to destroy or deactivate them, sometimes successfully. The rarity of snare injuries at Bossou may reflect not only recognition of the danger, but also possible inter-generational transmission of how to deal with snares [100,101]. Snared individuals sometimes receive help from others to get free [33,102]. Clearly, experienced chimpanzees know that snares are dangerous, and they empathize with snare-injured victims.

Humans drive vehicles, and these can kill chimpanzees. At Bossou, chimpanzee parties crossing a wide road that bisected their home range were usually large and contained the alpha male [103]. The chimpanzees visually scanned the road before starting to cross cautiously; parties with no adult male ran quickly to the other side. If an adult male was present he was usually first to scan and then lead the party onto the road, where he often stood 'guard' while the others crossed [104,105]. Chimpanzees crossing a road at Sebitoli in Kibale National Park also scanned in both directions; healthy adult males usually led the progressions and frequently guarded or checked on other individuals, especially trailing, 'vulnerable' members of the party [106]. Compared with Bossou, Sebitoli chimpanzees crossed in smaller subgroups, possibly an adaptive response to heavier traffic at this site. Despite their caution and vigilance, however, chimpanzees did not avoid crossing the road at points where visibility was restricted (e.g. at sharp bends). It seems reasonable to suggest that in the case of death following serious injuries as a result of getting caught in a trap or hit by a vehicle, survivors might make the association between physical injury and death.

(c) Nonhuman predators and other species

Mount Assirik chimpanzees responded with interest and vocalizations to visual or auditory signs of lions and leopards; they responded less intensely to hyenas and wild dogs [44]. More generally, responses to large cats vary from fear and alarm to overt aggression—at least towards leopards [43,107,108]. Taï chimpanzees chased leopards away on several occasions [33], and a radio-tracked leopard avoided noisy groups of chimpanzees [109]. At Mahale a party of chimpanzees pulled a leopard cub from a hole and killed it [110]. Wild-caught chimpanzees in Gabon were averse to leopard urine, but this response was lost in chimpanzees with high *Toxoplasma* loads [20]. Free-ranging West African chimpanzees vocalized loudly, and showed fear, 'reassurance frenzies' and aggression to stuffed leopard models, and used tools to attack them [111,112]. Survivors of non-fatal leopard attacks at Taï receive care from other members of the community, who lick and groom their wounds [33]. Together, these observations indicate chimpanzees' awareness of the threat posed by big cats, and of suffering in victims of predatory attacks.

Rare encounters with pythons elicited a combination of curiosity and fear in Gombe and Mahale chimpanzees [74,113]; snakes at Bossou elicited similar responses, and none was voluntarily touched [114]. Taï chimpanzees give distinct vocalizations when they see a python or a viper, and in field experiments individuals aware of the presence of a (model) viper called to inform ignorant companions approaching the snake [115,116]. Again, these behaviours suggest awareness that snakes can be dangerous, and also concern for others' safety. Yerkes [117] noted that young captive-born chimpanzees showed little fear of snakes compared with adults; normal, mature attitudes towards snakes are probably more heavily influenced by social learning than direct aversive experiences. Finally, there are no accounts of wild chimpanzees' reactions to live crocodiles, but a young wild-born captive showed no fear of water unless it contained crocodiles, for which he had no 'particular friendship' [118, p. 37].

(d) Other dangers

All or most chimpanzees likely experience painful falls, and see other others falling from trees. They clearly try to avoid falling, but it is not clear when they start to do so. Unlike monkeys [119] infant chimpanzees have never been tested on the 'visual cliff' apparatus used by psychologists to test various species' depth perception and fear of falling [120]. However, infants making exploratory excursions from their

mother sometimes fret about not being able to regain contact with her [121]. Mothers clearly guard against their infant falling: when moving in the canopy they carefully support the offspring with one hand or foot, or in the groin pocket by flexing one thigh [11]. They wait to help if older offspring struggle to cross a gap between branches, and quickly grab the youngster if it looks like falling; allomothers do likewise [40]. To avoid falling, chimpanzees must be constantly vigilant while moving around in trees; careful planning of arboreal routes might have been a selection factor in the evolution of self-awareness in large-bodied ancestral apes [122].

Chimpanzees are not good swimmers, and most avoid entering deep water [123], possibly for fear of drowning. The fact that many rivers and waterholes attract crocodile may add to wild chimpanzees' wariness of water, but at least one group regularly cools down in hot weather by soaking in a waterhole once [124]. The sign-language-trained chimpanzee Washoe once rushed to the rescue of another chimpanzee who was drowning in a moat. Washoe held on to a support, grabbed the other's arm and pulled her out of the water [60]. Again, this act suggests an understanding of the danger the other was in.

(e) Conspecifics

Like many other animals, chimpanzees show clear awareness that they can be hurt or injured, if not killed, by conspecifics. They employ a range of appeasement and reconciliatory behavioural mechanisms to control the amount of within-group aggression, including simple avoidance of potentially dangerous others, various gestural and tactile signals [74,125], and impartial interventions by third parties (policing) [126]. Participants in territorial boundary patrols are clearly tense, and they try to remain silent and inconspicuous [11,39,127]. This may indicate increased readiness for aggressive action against enemies while also reflecting fear of being detected and attacked.

5. Understanding death

Based on the above review of illness, injury and death in chimpanzees and how they respond to events and cues relating to these events, this section deals with the issue of the psychological significance of death for chimpanzees: how do they perceive it, and what is their understanding of it? The discussion is framed in terms of four elements or 'components' that typify adult humans' concept of death [128,129]: irreversibility (death is final; it cannot be undone), universality (all living things will die), non-functionality (dead individuals do not think, perceive or act) and causality (death results from non-survivable organ failure or damage). In addition to the literature already reviewed, it is important to keep in mind chimpanzees' known abilities in a range of relevant physical and social cognitive domains, including inferential reasoning, object permanence, self-awareness, metacognition, social learning, empathy, perspective-taking, mental attribution, cooperation and turn-taking [130–135].

(a) Irreversibility and non-functionality

By the age of 5 or 6 years most children view death as irreversible. Do chimpanzees share this view? Given the material already discussed it seems reasonable to suggest that sufficiently mature and experienced chimpanzees know that a dead individual will not come back to life. 'Sufficiently mature and experienced' here refers to adolescent or adult chimpanzees with direct experience of corpses and knowledge of how others respond to corpses. Unlike individuals who are asleep, regardless of what gets done to them dead individuals neither act nor react. This inert state often—although not always—occurs after one of the events leading to death reviewed above.

Here it is also worth considering that wild chimpanzees kill a variety of small-to-medium size animals including insects, reptiles, birds and mammals including other primates [74,82,83,136,137]; some are eaten opportunistically, others are deliberately hunted. Captive chimpanzees also capture and kill various animals (e.g., rabbits, squirrels, rats, birds, reptiles), which they often dismember and/or consume [138–140], although death sometimes appears to be an inadvertent consequence of rough, playful handling. In fact, all contact interactions between Bossou chimpanzees and other nonhuman mammals resulted in the death of the latter, which were often at least partially eaten ([114], but see [141]). All of these experiences seem likely to help chimpanzees construct the knowledge that death, once inflicted, is permanent, and that the dead individual is non-functional.

As mentioned in the Introduction, some chimpanzees simply disappear from their community without trace. Do chimpanzees, like researchers, infer that long-term absentees are dead? How to answer this question is not obvious, but it has been shown that chimpanzees remember long departed others for many years [142]. Future experiments might shed further light on chimpanzees' understanding of the permanence of death. In the meantime, however, a case can be made for reconsidering the widespread management practice of quickly and permanently removing seriously ill or dead individuals from their group, including freshly dead infants from their mothers. Might such interventions interfere with chimpanzees' evolved cognitive and emotional mechanisms for coping with death, including grief reactions [91,143]?

(b) Universality

Young children do not view death as universal; for them death happens to other individuals, not members of their own family or themselves. The universality component of the death concept is achieved by middle-to-late childhood. Unlike children, chimpanzees cannot be questioned directly, so whether they also understand that all creatures will die is not easy to determine. A useful distinction might be made between 'will' and '*can*.' As already discussed, adult chimpanzees in the wild may be well acquainted with death: family members and others die (or disappear); animals are killed for meat or other reasons, they get injured, and injured individuals sometimes die. It is conceivable that all of these experiences contribute to the formation of a category of 'animals that can die.' If such a cognitive category exists, how broad it is would be an interesting topic for research.

The notion of universality includes oneself, and integral to a mature human concept of death is the knowledge that *oneself* will die. Although chimpanzees have been credited with the capacity to know that they will die [144], there is no strong evidence for such knowledge, and in the absence of adequately language-competent chimpanzees it is hard to see how we could be sure. Again, it might be useful to

distinguish between 'will' and 'can.' Conceivably, given their experiences of others' deaths, and their own self-awareness [130], chimpanzees may understand that they could be killed by a predator, by falling out of a tree, or if attacked by other chimpanzees. However, alternative explanations for self-preservation behaviours can be proposed that do not require explicit knowledge of the reason for fear of dangerous situations. Three such explanations invoke fear of pain or injury rather than death itself, socially learning to fear specific stimuli without explicitly knowing why they should be feared, and the activation of 'evolutionary fears' that have evolved for their survival value, again without knowing why [145–147].

One striking consequence of humans' understanding of their own mortality is the ability to intentionally kill oneself [148,149]. Unlike many humans, however, chimpanzees do not deliberately kill themselves; nobody has ever seen a chimpanzee intentionally jumping to its death, drowning itself or ingesting a lethally poisonous substance. In some humans, ruminative and self-evaluative processes can lead to suicide as the chosen way to escape from unbearable psychological distress [149,150]. Despite their self-recognition abilities, however, there is no strong evidence that chimpanzees share the cognitive-emotional self-evaluations or real versus ideal self mismatches [151] that typify human self-awareness.

(c) Causality

Biological explanations of death come late in childhood. What knowledge do chimpanzees have about what causes death? It seems beyond argument that they know that they can inflict death on other creatures. Before eating smaller animals—including infant chimpanzees—they typically kill them by biting them in or around the head. Captured young colobus monkeys at Taï were invariably killed this way, whereas adult prey usually died only after chimpanzees began eating them, starting with the viscera [136]; live prey may be torn apart by several individuals competing for meat [33,137]. At Gombe, bites to the head were almost the most common way of killing small prey; bigger animals such as adult monkeys and juvenile bushpigs were flailed against a hard substrate [11]. In some cases death occurred only after chimpanzees started eating captured prey. With smaller prey the head region might be bitten first for fast access to the highly nutritious brain [152]. The predominance of this killing method led Videan *et al*. [138] to comment on the deliberateness of the act. The ontogenetic emergence of the 'craniocervical killing bite' in various predatory species including primates [153] merits further study, as does the development of killing (or stunning) larger prey by flailing them against a hard substrate [11,137].

With regards to the causality component of the death concept it is noteworthy that descriptions of lethal attacks on adults often mention wounds around the throat and genitals of the victim (in males the testicles are sometimes severed), along with various other crush, slash and puncture wounds [39,66–68,71,154]. Death is usually attributed to shock and loss of blood. It is tempting to speculate that adult chimpanzees target the throat because damage there can cause profuse bleeding. In any case, the range and flexibility of ways that chimpanzees kill suggest some rudimentary knowledge about biological causes of death.

The causality issue also arises in the frequently cited case of Flint, an 8-year-old Gombe male whose demise has been described as an example of a chimpanzee losing the will to live [11], or fatally 'shutting down emotionally' [143]. Although physically healthy, Flint was unusually emotionally dependent on his mother. After her death he became increasingly lethargic and withdrawn; he refused to eat, and died three weeks later [155]. Was it suicide? Although Flint was clearly depressed, deliberately bringing about his own death in this manner would have required (a) the abstract causal knowledge that starvation causes death and (b) some reason for preferring this method to an alternative, such as jumping from a tree. As described earlier, non-avoidance of disease victims may reflect a lack of awareness about slowly acting causes of death such as contagious diseases. Before they attain a mature biological concept of death children tend to focus on observable external causes, such as guns or cars. Whereas chimpanzees appear likely to associate some specific external events with death (e.g. violent attacks, guns, predators, falls), there is no evidence for awareness of the link with less obvious causes, such as disease or starvation.

6. Questions for future research and conclusion

There is still much to discover about behavioural and psychological reactions to death in chimpanzees, including their understanding and feelings about death. One obvious question is whether they show any evidence of human-like taboos about killing. They clearly relish killing and eating other animals, and sometimes show no qualms about starting to eat their prey alive (many humans also have no moral issues about eating or cooking live animals), but do chimpanzees have a moral code against killing other chimpanzees? It can be assumed that most chimpanzees are not murderers, but killing sometimes appears to be acceptable, as in some territorial encounters and cases of infanticide. Similarly, although some individuals actively refrain from participating and may even try to protect the victim of lethal gang attacks [68,69], others do not hesitate to join in. Precisely how outbreaks of collective lethal violence come about in chimpanzees is unknown, or when conspecific killing is 'acceptable' and when it is not. The only pertinent experimental study to date asked whether intra-species infanticide might be perceived as a violation of a social norm: 'infants should not be harmed.' Captive chimpanzees watched video clips of unfamiliar chimpanzees (1) aggressively attacking and killing an infant, (2) hunting a small colobus monkey, (3) showing nonlethal aggression among adults and (4) nut-cracking [156]. Although chimpanzees looked longest at the infanticide scenes, there was no evidence of heightened emotional arousal during these presentations. The authors suggested that unfamiliarity of the chimpanzees in the clips might have dampened any emotional responses. Combined behavioural and physiological studies of responses to death-related stimuli could be useful for learning more about affective responses to death.

What about the morality of cannibalism? Are dead chimpanzees simply perceived as potential food, like captured bushpigs or monkeys? The answer appears to be no. First, most dead chimpanzees do not get cannibalized. Second, less of the corpse of cannibalized infants is consumed compared

Table 1. What chimpanzees might learn from experiences of death and death-related contexts, and possible contributions to their understanding of four cognitive components of a death concept.

		contribution to cognitive component of death concept?			
danger/death context	potential learning	irreversibility	non-functionality	universality	biological causes
disease	Sick individuals may weaken, die. No avoidance of diseased or dying others. Some empathic responses.	no	no	no	no
injuries	Injured or wounded may die. Injuries and wounds are painful. Injured and wounded may receive care.	no	no	yes	possible
humans	Humans sometimes injure, kill. Snares, traps, vehicles also injure, kill. Caution and evasive action often required.	yes	no	no	possible
predators	Predators and some other species (e.g. snakes) can injure or kill. Caution and evasive action often required. Aggression sometimes appropriate.	yes	no	possible	possible
accidents	Falls from trees can injure, kill. Deep water is dangerous. Caution, avoidance required. Help given to others (e.g. youngsters) in difficulty.	yes	no	possible	possible
conspecifics	Chimpanzees sometimes injure, kill, eat others. Avoid getting attacked. It is possible to kill.	yes	yes	yes	possible
non-predatory animals	Other animals die, get killed, eaten. It is possible to kill animals, using different methods.	yes	yes	yes	possible
corpses	Corpses do not act or react. Corpses never come back to life.	yes	yes	possible	no

with similar-sized monkey prey [81], suggesting a psychological difference between eating a conspecific and another species. Third, intra-community infants are eaten less completely than extra-community infants [81]. The psychology of cannibalism in chimpanzees requires further study.

In many humans, from late childhood a fifth element of the death concept takes on increasing importance, namely, the notion of some kind of afterlife, sometimes referred to as a metaphysical concept of death [157,158]. Chimpanzees have been prematurely described as engaging in 'ritual practices' in in the presence of dead conspecifics, contributing to evidence of an analogue to human religion [159]. However, although death in chimpanzees appears psychologically more impactful that death in other species, compelling evidence for any notion of a spiritual life after bodily death in chimpanzees is not forthcoming.

As reviewed above, chimpanzee responses to conspecific deaths are highly variable and include frenzied excitement, loud vocalizations, displaying, attacking and rough treatment of the body, consuming it, tending it carefully, sitting quietly and looking at it, making soft vocalizations before abandoning it and, especially in the case of deaths of unknown cause, partly covering it with vegetation [33]. Some individuals have been seen to return to where they last saw the body of a familiar conspecific [68,71]. Systematic comparisons of reactions across communities remain to be conducted. Like many other behaviours [123,160], responses to death might show cultural variations (see [72] for one suggested example).

In conclusion, chimpanzees, in common with many other animals, strive to stay alive by avoiding potential causes of death or minimizing risks. Their experiences with death in other chimpanzees and other species—including individuals they have killed themselves—may well contribute to construction of a human-like understanding that dead individuals no longer behave or feel anything (non-functionality), and that they will stay dead (irreversibility) (table 1). As in humans [157], direct experience of death in childhood possibly facilitates maturation of the death concept in chimpanzees. Chimpanzees—and probably other great apes—understand that death 'is different from life and permanent' [161, p. 196]. Taï chimpanzees groom and lick wounds of injured, but not dead kin and companions [33]. Whether chimpanzees understand that all creatures will die (universality) is less clear, but a reasonable suggestion is that they know that other creatures can die. This knowledge probably includes a notion of their own vulnerability, if not the inevitability of their own death. Although there is little evidence for a mature human-like understanding of the 'biology' of death (causality), they do have some knowledge about effective ways of killing, which they apply to conspecifics and other targets flexibly (see [162] for another example of flexibility in killing techniques). Comparative evolutionary

thanatology needs more information on nonhuman species, not least to improve our understanding of the evolution of our own species' psychology of death [163–165]. Primatologists clearly have a role in this endeavour. In view of the precarious survival prospects of many great ape populations, we must hope that valuable information on how death is dealt with and represented in great ape communities can be discovered before their cultures die out.

Data accessibility. This article has no additional data.
Competing interests. I declare I have no competing interests.
Funding. I received no funding for this study.

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