# Comparative Thanatology of Primates:

# Historical, Evolutionary and Empirical Approaches

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# Contents

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# Section 1. A Historical account of comparative thanatology

# Chapter 1. Thanatology: the study of life, with death left in

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*"No one presupposes that one of the lower animals reflects whence he comes or whither he goes- what is death, or what is life and so forth. But can we feel sure that an old dog with an excellent memory, and some power of imagination, as shown by his dreams, never reflects on his past pleasures in the chase? And this would be a form of self-consciousness."*

*"It is often difficult to judge whether animals have any feeling towards others' sufferings. Who can say what cows feel, when they surround and stare intently on a dying or dead companion?"*

Charles Darwin [1871, *The Descent of Man*, p. 60; 73]

*"[Researchers] state without qualification that man is the only animal that can be aware of his own future death. But I suggest that we pause and ask just how anyone knows this. What sort of evidence is available either pro or con?. (…) The available negative evidence supports at most an agnostic position."*

Donald Griffin [1976, *The Question of Animal Awareness*, pp. 104–105]

## 1. Introduction

Humans are peculiar among primates for the fact they have been burying their dead since at least 120.000 years ago and using alternative ways of disposing of them for even longer, according to the archaeological record (Stiner, 2017; Pettitt, 2011). And while it is true other non-human animals have been documented engaging in *burying behaviors*, the underlying causes/motivations behind these vary substantially; they are either reflexive, accidental, or incidental and do not have the distinctly deliberate character of human mortuary behavior (Gonçalves & Tomonaga, 2021).

Throughout history, the idea of humans as distinct from other animals not only in *degree* but sometimes in *kind* is encountered time and time again in written sources sharing an intellectual tradition that reaches as far back as ancient Greece. The definition of humans as distinct *rational beings* derives from the medieval term "*animale rationale*" which has its origin in Aristotle's formulations of humans as the *zōon politikon* (political animal) and the *zōon logon echon* (language possessing animal). Indeed, for better or worse, aspects of this thinking permeate even today as human civilization yielded cultural, technological, and socio-economical advances unprecedented in our planet's history. Grounded in capacities such as tool-use, language, cumulative culture, and symbolic thought, humans gave rise to music, art, literature, legal codes, ethics, religion, science, and other institutions transcending the temporal boundaries imposed by our individual finite existence.

Awareness of death, too, has been explicitly or implicitly regarded as defining trait of *Homo sapiens* by authors in several schools of thought from *philosophy* (Rousseau, 1755; Schopenhauer, 1818; Heidegger, 1949), *anthropology* (Morin, 1951; Becker, 1973), archaeology (Leroi-Gourhan, 1993; Tattersall, 1998) to *biology* (Dobzhanksy, 1967; Gould, 1997) and *psychology* (Kastenbaum, 2000). These claims are usually presented under the assumption of human exceptionalism and while they appear self-evident, they have not been without challenges.

It was with Charles Darwin that a strong case for a psychological continuity with humans and other animals was made (Darwin, 1871; 1872). Separated by a century, both Charles Darwin and Donald Griffin both expressed doubts regarding to which extent non-human animals could comprehend death. Their questions are different in nature; unlike Griffin, Darwin did not ponder the question of whether animals conceptualized their own mortality but rather modestly, to which extent they recognized and how they "felt" in response to death in their midst.

Questions such as these are at the forefront of the recent field of *Comparative Thanatology* which, for the past decade or so, has concerned itself with the scientific study of responses towards death in non-human animals at the psychological, behavioral, social, and physiological levels (Anderson, 2016). Recent scientific interest notwithstanding, responses towards the dead in non-human animals have been observed since at least classical antiquity, but are even found in Homeric epics (Akexandritis, 2010). Most notably, Aristotle (384-322 BC), Lucretius (99-55 BC), Apollonius of Tiana (3 BC–97 AD), Pliny the Elder (AD 29-79), and Claudius Aelianus (AD 175-235)[1] recount stories of dolphins assisting their dead companions to the surface, cows grieving for their slain calves, seals carrying/stationing around dead pups, or ants and elephants burying their dead. Fast-forwarding to the 18th and 19th centuries, first-hand reports and anecdotes accumulated replacing or reconfirming previous legends on non-human animals' responses to their dead. Responses ranging from protection to transport of the body, vigils, and emotional distress at times with allusions to grief were attributed to non-human primates, proboscideans, cetaceans, corvids, ungulates, carnivores, and sirenians. Poignantly, increasingly more observations comparable to these have been recently corroborated by researchers in many of the same taxa (Gonçalves & Biro, 2018; Gonçalves & Carvalho, 2019).

In 2016, the field was given a formal name: comparative thanatology. A year that coincidentally, also marked the 100th anniversary of the death of a Russian scientist and Nobel laureate Elie Metchnikoff (1845-1916). Metchnikoff had been a zoologist by training but in his later years, becoming concerned with the need for a scientific study of death and aging published books on this matter and in the process coined the term thanatology[2] from the Greek *Thanatos* (death) and *logos* (study of) (Stambler, 2015). Thanatology once defined by Kastenbaum (2000) as "*the study of life with death left in*" only flourished as an academic field during the post-war

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[1] See *Aristotle's The history of Animals* (1883 translation); *Lucretius' On the Nature of Things* (1883 translation); Philostratus's *Life and Times of Apollonius of Tiana* (1922 translation); *Pliny's Natural History* (1938 translation); *Aelian's On the Nature of Animals* (2011 translation).

[2] This is the prevailing account seen in many thanatology-oriented publications. In fact, the term *thanatology* as "*a description or the doctrine of death*" can be found as early as 1843 in *A New Dictionary of Medical Science and Literature* penned by British-American physician Robley Dunglison. "La theorie de la mort, que nous nommerons thanatologie, fera donc partie de la science qui nous occupe; elle complete l'histoire des operattions du principe vital dans les maladies" in 1829 from the *Traité d'anatomie pathologique: L'anatomie pathologique génerale* by the French pathologist Jean Frédéric Lobstein.

period. The need for a comparative approach began to emerge more concretely with James Anderson and colleagues when they published a critical article on chimpanzees' behaviors towards a dying and after the death of an elderly female that would prove decisive both in catalyzing widespread interest and establishing a formal field (Anderson et al., 2010). But to argue serious interest only emerged after this publication would be an oversimplification. Using chimpanzees as an example; wild chimpanzee scholarly work has had a tradition, starting with books such as *The Chimpanzees of Gombe* (Goodall, 1986a), through *The Chimpanzees of the Taï Forest* (Boesch & Boesch-Archermann, 2000), and continued in *The Chimpanzees of the Budongo Forest* (Reynolds, 2005), followed by *The Chimpanzees of Bossou and Nimba* (Matsuzawa, 2011) and *Mahale Chimpanzees* (Nakamura et al., 2015), in which in all of these, death responses in chimpanzees are treated in detail with their sections/chapters. This fact has been acknowledged repeatedly in Anderson's publications (Anderson, 2011; 2020a). Indeed, as Anderson and colleagues point out in their original 2010 paper, written records concerning animal responses to death reach far back into the past, cited in their paper is the first observation published in an academic paper about grief in a captive chimpanzee (Brown, 1879), and it is worth pointing out that the first scientific paper on dead infant carrying in a captive rhesus macaque, dating from the early 20th century (Yerkes, 1915).

More recently, comparative thanatology has been featured in two special journal editions in *Philosophical Transactions of the Royal Society* (Anderson et al., 2018) and *Primates* (Anderson, 2020a) and also one academic book, *Evolutionary Perspectives on Death* (Shakelford and Zeigler-Hill, 2019). In addition, it has been the focus of at least two academic events; *The Kyoto Workshop on Evolutionary Thanatology* and *CARTA Awareness of Death and Personal Mortality: Implications for Anthropogeny* (see Figure 1). Finally, this subject has also recently been the main topic of both Masters and Doctoral theses (Bracebridge, 1998; Iglesias, 2012; Fiore, 2013; Swift, 2018).

Missing in the comparative thanatology discussion is the fact that Metchnikoff, in his book, briefly discussed the possibility of a concept of death in non-human animals:

> *"Among lower animals the preservation of life is accomplished without mental connivance, conscious or unconscious (...). All these devices for the avoidance of danger and escape from death could have been developed in animals before these had any distinct idea as to what death was. We know that some animals can distinguish between living and dead prey. Some carnivora recognise the smell of dead bodies. Those which are accustomed to feed on the living creatures refuse all others, detecting the difference by the absence of movement. As in such cases the idea of death is imperfect, it is easy to deceive the creatures by offering carcases artificially set in motion, or living prey rendered motionless (...), many insects when alarmed become motionless and feign death (...). Moreover, the higher animals, such as mammals exhibit a profound ignorance of death, many of them remaining completely undisturbed by the presence of dead companions (...). However (...) there are others that instinctively shrink at seeing the dead bodies of their own species. Horses on passing a dead horse show signs of discomfort, and attempt to run away- Bullocks when witnessing the slaughter of others, also exhibit evidences of distress and fear. In spite of these examples however, it is quite certain that animals, even those highest in the scale of life, are unconscious of the inevitability of death, and of the ultimate fate of all living things. This knowledge is a human acquisition."*
>
> Elie Metchnikoff [1903, *The Nature of Man*, p. 114-115]

Whereas Metchnikoff, favored the acquisition of the concept of death as an exclusively human affair, he did credit non-human animals with the ability to discriminate live from dead animals. From an evolutionary perspective, such "discriminations" could be advantageous since corpses are a potential source of critical information; they can be a food resource, they can signal predation events, or they can be a pathogen hazard. Particularly in vertebrates, a constellation of behaviors ensues around dead conspecifics and the sensory death-cues associated with them ranging from avoidance, emotional turmoil, alarm-calling, to gathering around and physically manipulating the corpse. Consequently, by observing our closest primate relatives and further down the evolutionary path, we can begin to glimpse responses that came before our elaborate ways of treating and conceiving the dead and recognize the evolutionary pressures behind these both at the levels of convergence and divergence.

## 2. Previous empirical approaches to comparative thanatology

Although some insights originated from experimental settings (i.e. grief research, scavenging/predation, or infanticide), have contributed to the field of comparative thanatology, additional experimental work merits further exploration here:

*The stuffed/fresh corpse paradigm*. Introducing a recently dead or stuffed primate to record other living primates' reactions can ultimately be traced back to the seminal experiments on fear performed by Hebb (1946) and Butler (1964) (see Chapter 3 p53).

Mirelle Bertrand, primarily researching stump-tailed macaques (*Macaca arctoides*), presented two recently dead stump-tail females (an adult and juvenile) to captive groups of stump-tailed macaques, rhesus macaques (*Macaca mulatta*) and lion-tailed macaques (*Macaca silenus*) soon after death, then, 1 and 2 days later for a period of 30 minutes. Similarly, a dead adult lion-tailed macaque was presented to these groups. According to her, all the monkeys showed an initial interest, but in contrast to a living monkey, they sniffed them more and did not threaten them nor displayed facial expressions at them. One of the stump-tailed males tried to mount the dead adult female and dragged her around as he did when she was alive, Bertrand points out. The stump-tailed group groomed all three corpses considerably but the author explains it was different than social grooming; one would groom her with a foot on her face, another touched her open eye and by the third day, they were removing chunks of fur and groom those. Another response she noted was that all groups were more cautious with unknown monkeys whether from the same species or other, approaching and touching immediately a dead member they knew. Bertrand also presented a stuffed langur (*Semnopithecus sp.*) in a quadrupedal position and bared its teeth to all three species to which all reacted as if it was a live threat (threatening, grinning, lip-smacking, averting eyes, and running away) but also smelling it. The rhesus and the lion-tailed macaques were also more cautious than the stump-tails but for a few hours among all groups it was ignored (Bertrand, 1969).

Finally, Kaplan (1973), researching captive squirrel monkeys (*Saimiri scireus*) presented 19 dead infants to 15 adult females in weekly trials. His experiments revealed that mothers whose infants had died from birth to one week displayed a more generalized strong response to the infants presented to them (either their own or others), while mothers whose infants had died from 2 to 6 weeks showed a more discriminate response being stronger to their own infants and weaker to others that were not. Thus his research suggested that squirrel monkey females became increasingly more selective towards their infants as time passed after parturition while other perceptual cues such as infant size were also involved, these results were in accordance with other mother-infant recognition experiments conducted during the 1960s onwards (reviewed in Maestripieri, 2001).

*The anesthesia paradigm*. A live anesthetized individual is significantly comparable to a dead one: it does not move and is unresponsive to outside stimuli. Hebb (1946) also pioneered this approach; in his chimpanzee group, a low-ranking anesthetized adult conspecific produced avoidance, aggressive, and fearful responses. Subsequent research focused more on mother-infant bonding.

Rosenson (1977) featuring three species of lemurs (*Eulemur fulvus, Eulemur macaco, Lemur catta*) and a galago (*Galago crassicaudatus*) observed their reactions towards their anesthetized infants. While none of them attempted to pick them up or carry them, the galago mother retrieved the infant with her jaws and dropped it when attempting to groom, also the black lemur mother was seen gripping and lifting her infant. Grooming was observed in all the mothers and most were in regular contact with the infants but once the infants regained consciousness the females rejected them, possibly due to the infant's initial abnormal locomotor activity. Unsurprisingly, macaque mothers do carry their own anesthetized infants, both bonnet (*Macaca radiata*) (Rosenblum & Youngstein, 1974), and long-tailed macaques (*Macaca fascicularis*) (Negayama, 1988).

*The playback call paradigm*. Allen & Hauser (1991) concerning themselves to explain concept attribution in non-human animals dedicated a great part of it using cognizance of death as an example. They proposed an experiment using the playback call paradigm on vervet monkeys (*Chlorocebus aethiops*) of their recently dead infants. The females, they argue, when presented with the playback would (1) orient themselves to the speaker and act as if the infant were alive, (2) respond in a distressed manner by initiating a search for the infant, or (3) not react at all and continually engaging in their activities.

This has never been tried with primates as far as we know, possibly due to ethical concerns, however, a close variation to Allen & Hauser’s experiment was done by Palombit et al. (1997) in free-ranging chacma baboons (*Papio ursinus*) where they tried to access the strength of male-female relationships. The experiments consisted of a playback of a female’s scream to a *male friend* or a *control male* of similar rank, the rationale being that friend male baboons would at times come to aid a screaming female more often than non-friends. During the study period, 16 of

21 infants died, so it was possible to resume the same playback call after the female's infant had recently died (within 1 to 4 weeks) to the male baboons. What they found was a sharp decline in all the *male friends'* responses when compared to their same responses while the infants were alive and their responses were significantly lower than the *control males*. Also, when playing the female's scream or a control female the *male friends* no longer exhibited a strong response to the first in comparison to the former (orienting towards the speaker versus ignoring). Palombit et al. (1997) point out that these responses coincide with a sharp decline in spatial associations between those females and their male friends after the infant had died. This is because females were chiefly responsible for maintaining close associations with the males so it is likely that the females ended the friendships after their infants died if this was because they no longer needed a male to protect their infants or that they themselves no longer benefited from the protection of the male is, according to the authors, unclear.

*The hormone collection paradigm*. The death of a female baboon (*Papio h. ursinus*) due to lion predation produced a subsequent altered behavior of her mother. During the following days, this high-ranking female remained distant from her group and never initiated social interactions. Because of this, and the fact that baboons form close knit-groups between related females (matrilines), it compelled researchers to collect fecal samples to measure stress hormone levels (fecal glucocordicoid) plus focal behavioral data on the females after death had occurred in the troop (King, 2013). After recording a total of 26 deaths, Engh et al. (2006) found that stress levels were particularly high for females who lost a relative, mostly in the first weeks after in comparison to the weeks before with control females showing no such response. Additionally, these "bereaved" females seemed to compensate for the loss of kin by widening and reinforcing their grooming network. Engh and colleagues suggest this would have made their stress levels return to baseline. Cheney & Seyfarth (2013) extended this research by examining how individual differences played a role in the response of females. Temperaments, either “aloof”, “loner” or “nice” were attributed to them. They found that, in the span of two weeks, “loner” females, were unsuccessful in building newer relationships and their stress levels increased significantly in contrast to “aloof” and “nice” females who increased their grooming network and decreased their stress levels.

While doing behavioral experiments in tandem with a daily sampling of cortisol in saliva from common marmosets (*Callithrix jacchus*) Kaplan and colleagues, witnessed the fatal accident of a female that fell from a branch and broke her spine. This rare event captured in the laboratory was sampled at the hormonal level. According to researchers, the cortisol levels rouse in the group and when they would decline (during the afternoon) stood up and remained high for three days (Kaplan et al., 2012).

### 2.1. Strengths and Limitations of Current Paradigms

For a long time, *the ethological paradigm* (i.e. naturalistic observations) has served and continues to serve a central role not only in describing elusive behaviors surrounding death but in generating new hypotheses that might in turn explain them. However, its greatest attribute is also its greatest weakness: while highly suggestive, because they are rare and occur in uncontrolled environments it is problematic to advance any theoretical framework associated on account of anecdotal evidence, specifically the early cases. Nonetheless, the possibility of video-recording rare events on tape such as responses to death (Muller et al., 1995; Matsuzawa, 1997; Anderson et al., 2010) while not solving its problems, does elevate the *anecdote* to a *single observation*, thus making it available for scientific scrutiny, which can, in turn, generate scientifically sound data (Matsuzawa, 2011).

Waiting for the unfortunate but fortuitous death of an animal can require large amounts of observation time both in the field and in captivity. The fresh/stuffed corpse paradigm eliminates this predicament by situating the stimulus near the group at a set time and place chosen by the researcher. Comparable results to the *ethological paradigm* have been obtained using fresh or stuffed corpses of conspecifics. While much research under this paradigm was realized in uncontrolled experiments (Hebb, 1946; Bertrand, 1969; Kaplan, 1972), there is room for improvement like testing further variables such as fresh versus decomposed corpse or complete versus disrupted corpse, and so forth. The major challenge of this experimental method in replicating the ethological observations is that, unlike the latter, the dead conspecifics will frequently be unknown to the group which could impact their response. The alternate method could prove nearly unfeasible, both logistically and ethically speaking, since it would involve removing either a living or dead conspecific from its group only to present it later on. Dead individuals unknown to the group need not be a limitation but may also present an opportunity to decouple emotional outbursts from investigative curiosity among the living.

The *anesthesia paradigm* is similar to the previous one, instead of an actual corpse, a living immobilized individual is used. A convenient approach that still presents restrictions since unconscious does not equate to dead. Several cues are present in the first that cease in the second (breathing, body heat) and these will likely be discerned by the living. Additionally, anesthesia only lasts for a limited amount of time limiting the observation duration. Thus, only very limitedly does it inform us on how primates process death.

The *playback call paradigm* has, in general, presented strong and compelling data from the field (Cheney & Seyfarth, 1990; Seyfarth & Cheney, 2007). However, the specific experiment suggested by Allen & Hauser (1991) presents ethical concerns as it may potentially cause distress in the mother of the dead infant. The variation of Palombit et al. (1997), does present a rather optimistic prospect for testing awareness of death. Variables such as the mother carrying the infant or not at the time of the playback call could prove significant. It remains a fact that playback call experiments are notoriously difficult to carry out (setting up the experiment and waiting for the right conditions).

The hormonal paradigm can potentially yield the most robust data by measuring glucocorticoid levels to measure stress in the individual. Of course, observing and measuring emotional responses in the form of stress or grief are important and informative in the way they show us how primates react to the loss of a conspecific known to them both externally and internally. But these are parallel to but not directly tied with effects such as the formation of a concept of death. Nevertheless, given the astonishing variability in the duration of dead infant carrying behavior (Sugiyama et al., 2009; Fashing et al., 2010), looking for Gc (glucocorticoid) levels in these females could prove a worthy scientific endeavor as we do not yet know if and how these vary between them.

## 3. Current Research Objectives & Approach

### 3.1. Aims of the study

In this thesis, I sought to identify patterns of similarity and variation between non-human primates and both chimpanzees and humans. This took the form of two literature reviews in targeted at non-human animals broadly and non-human primates more specifically present in Chapter 3 and Chapter 5 respectively.

In Chapter 3. I looked at evidence of thanatological reactions in non-human animals from the past and the present, categorizing them into direct contacts (physical touch with the body) and secondary interactions (guarding the corpse, vigils, and visitations). I examined the cues that these species employ to distinguish between life and death in others, as well as the proximal and ultimate drivers of their capacities to do so, using information from comparative perception and cognition research (with an emphasis on corvids, proboscids, cetaceans, and primates). Like agents, corpses have static cues of animacy (such as shape and texture), but like objects, they lack dynamic cues (self-propelled motion and contingency). I proposed the term *animacy detection malfunction*, to refer to the conflicting cognitive processes when encountering a corpse, caused by visual mismatches that cause expectation violations. Additionally, in Chapter 4, using the same reviewing methodology, I assessed the evolutionary drivers of grief with a focus on mammalian taxa of which there appear to be deep homologies. Likewise, Chapter 5 focuses on non-human primates, given that there is a significant gap in the fossil and archaeological record regarding how early humans lived extant primates may provide vital insight into how and in which hominins dealt with their dead. In it, I proposed an integrated model of Life-Death Awareness in which the agency system utilizes brain circuitry dedicated to recognizing life.

In Chapters 6 and 7, I ran a number of eye-tracking experiments to find out how chimpanzees respond to stimuli that are associated with death. In the first series of experiments, I reasoned that since chimp faces are seen similarly to chimp skulls, they will be subject to the same biases. In general, the chimpanzees favored conspecific-related stimuli (particularly chimpanzee faces and skulls in forward-facing and to a lesser extent diagonal orientations), and they paid more attention to the teeth. I contend that chimp skulls still have significant, human-like features that cause their brains to activate a domain-specific face module, focusing their attention. In the second series of experiments, one method involved using dynamic stimuli (videos) depicting chimpanzee-only agents interacting with each other with both alive and dead group members. These videos were also played together with “positive” *versus* “negative” chimpanzee vocalizations to test whether chimpanzees would match negative vocalizations with videos of dead chimpanzees. The results thus far, have not shown any tangible results. A third method involved showing images of both living and dead animals. The findings show that chimps notice living "standing" animals more quickly than dead "prone-supine" animals, supporting the animate monitoring hypothesis and similar findings from other eye-tracking studies on humans. This was further supported by a follow-up experiment using primate-only image stimuli depicting live and dead-infant carrying: the chimpanzee subjects also exhibited a significant looking preference for live infants over dead ones.

## 3.2. Ethical Concerns

There are ethical concerns that manifest concerning thanatological research with long-lived animals imbued with intelligence and possessing complex emotional lives. David Premack notably commented on his chimpanzee research:

> *“Unlike man, however, they do not know that they will die. Can I tell the ape that it will die? Could I arrange procedures that would culminate in a knowledge of death? If we succeeded in communicating this information to even one animal, saw its hair stand on end, heard it moan, we would know we had provided the necessary conceptual*

*elements which the animal combined to make this knowledge possible. And we would have proved that the limits of the ape's concept of self-approach more closely our own than had been thought. But we cannot take such pedagogy lightly. What if, like man, the ape dreads death and will dread with this knowledge as bizarrely as we have? (...) The desired objective would be not only be that of dread, which, in the human case, has led to the invention of ritual, myth and religion. 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).

Contrasting Premack's assertion, it is not part of the research agenda to ascertain if monkeys or apes have an awareness of their mortality or to instruct them on such knowledge,

rather, the research agenda is concerned with ascertaining whether non-human primates make a clear distinction between living (a live agent) and non-living (a dead agent) when confronted with it, and methods it aims to utilize are non-invasive. This approach is supported by previous research, for instance, Butler's research condition with the dead conspecific failed to provoke fear in the rhesus monkeys subjects which he attributed to a "psychological barrier" between the subjects and the fear-stimulus (Butler, 1965). A more recent study by de Rohr et al. (2015) presented captive chimpanzees with recorded videos of infanticide involving unfamiliar conspecifics which failed to create any marked emotional reactions in its watching subjects possibly due to the same reason.

### 3.2. Non-invasive eye-tracking approach

The *looking time paradigm* has its roots in the 1950s and 60s research of Robert Franz in child psychology. Despite all its differing methodologies, the paradigm itself is fixed into a common assumption that the subjects will look longer at stimuli presented that are, for whichever reason the most interesting to them. For this research, there are two key methods of interest within the *looking time paradigm*: the *violation-of-expectation task* and *the visual bias task*. These tasks can be recorded by either the experimenter recording looking times with a chronometer, by video recording followed by later coding and more recently with eye-tracking technology. The *violation-of-expectation task*, as the name suggests posits the individual will look longer when visual scenes do not conform to its conjectured view of both the physical and the social realm. The *visual bias task*, on the other hand, has several stimuli presented simultaneously or consecutively, the visual biases will then be measured based on the looking time prompted by each stimulus (reviewed in Winters et al., 2015).

The looking time paradigm has also been used in primate research for such varied studies as self-recognition (Anderson et al., 2009), goal-directed behavior (Myowa-Yamakoshi et al., 2012), and face processing (Kano & Tomonaga, 2011). Using an eye-tracking methodology that is accomplished by either head mounting or external mounting both relying on optical eye-tracking, especially the latter methodology (which is the least invasive) has produced results (Kano & Tomonaga, 2009; Hirata et al., 2010; Myowa-Yamakoshi et al., 2012; Kano & Tomonaga, 2013, Kano & Hirata, 2015; Krupenye et al., 2016).

# Chapter 2. Comparative thanatology: connecting the historical dots

*"Two persons were on a journey, and passing through a hollow way, a dog, which was with them, started a badger, which he attacked, and pursued till he took shelter in a burrow under a tree. With some pains he was hunted out, and killed. (...) They had not proceeded far, when they heard the cry of an animal in seeming distress, and stopped to listen whence it proceeded, when another badger approached them slowly. They at first threw stones at it; notwithstanding which, it drew near, came up to the dead animal, began to lick it, and continued its mournful cry. The men, surprised at this desisted from offering any further injury to it, and again drew the dead one along as before; when the living badger, determined not to quit its dead companion, lay down on it, taking it gently by one ear, and in that manner was drawn into the midst of the village; nor could dogs, boys, or men induce it to quit its situation by any means; and, to their shame be it said, they had the inhumanity to kill the poor animal, and afterwards to burn it, declaring it could be no other than a witch."*

Thomas Brown [1835, *Anecdotes of the Animal Kingdom*, p. 412-413]

Detailed published records in academic journals from the 19th century and before are rare. As with the badger anecdote related above, most of these accounts come in the form of travelers' tales, local legends, or from exotic pets acquired through the pet trade, usually depicting human encounters with these animals invariably, sooner or later, ending in their demise. While many reports are sprinkled with anthropomorphism, to the credit of the authors, they humanize their animal subjects often portraying them as individuals with emotional lives and evoking pity with the acts against them condemned or lamented (as seen from the badger anecdote recounted above).

## 1. Early Descriptions in Birds

Reports on birds, often involving monogamous pairs depict a recurring behavioral pattern: when one of the pair (or flock) is killed the other conspecific vocalizes in apparent distress and engages in physical interactions towards the dead body presumably to elicit a response or to carry it away from perceived danger. An anecdote of the now-extinct paradise parrot (*Psephotellus pulcherrimus*) recounts a female that flew to her dead mate after he was shot lifting his head with her beak and rolling the body before flying away and returning with straws that she then placed next to him possibly as food, who then was also shot down as a mercy killing (Lumholtz, 1889). The same spectacle is echoed in a report concerning lesser terns (*Sternula albifrons*): after one in the couple was shot, the remaining gave out "plaintive cries" and flew over the body calling with "every accent of distress and grief", attempting to seize the partner by its beak and carry it: in the end also killed out of mercy (Stevenson, 1890). Similarly, it had been noted in their relatives, the black terns (*Chlidonias niger*) would similarly give out distress cries and plunge as if to defend their dead group member (Heermann, 1859). And yet again with a gray catbird (*Dumetella carolinensis*) who started pecking at the neck feathers of its presumed mate's corpse attempting to lift it and shaking it giving out "a moan of gentle sorrow" (Elliot, 1883). Another anecdote concerning the extinct South Island kōkako (*Callaeas cinereus*) which hoped around its dead mate and called in "a great state of agitation", this time the tracker who was "very sorry" let the remaining mate go (Hughes, 1886). A hunting guidebook notes that when rooks (*Corvus frugilegus*) are shot, instead of fleeing they circle around its dead companion "uttering cries of distress", appearing to show anxiety and sympathy for the fallen group member, but when in one case the corpse was hung to a stake, it was visited by the group members once, then afterward left the field permanently (Maxwell, 1833). Likewise, another hunting guidebook advises, when golden plovers (*Pluvialis apricaria*) are concerned to bring two guns since when one of the kind is killed, the flock will come back and hover over the body (Cox, 1866). Other species are noted to exhibit a similar concern for the dead group member and could be killed in the same fashion including Common gulls (*Larus canus*) (Blake-Knox, 1867), Northern lapwings (*Vanellus vanellus*), and European golden plovers (*Pluvialis apricaria*) (Eadem, 1876). Where previously such descriptions appeared in newspapers, monthly magazines, and memoirs, they also start appearing in peer-reviewed journals. In *The Auk*, George Mackay gives a comprehensive portrayal of the behaviors of the long-tailed duck (*Clangula hyemalis*) finishing the account with a commentary on the attachment of a female duck to its mate which Mackay had shot; she swam up its mate returning four times, “continually honking and calling at him” before being herself shot. Mackay further notes, that while there were other members of the flock nearby, which the female passed when she was engaging in her back-and-forth behavior towards the dead male, she still would not leave him to join the flock. This response, he considered unusual, noting the inverse (live male to dead female interest) was more common among waterfowl (Mackay, 1892).

## 2. Early Descriptions in Mammals

Owing to the increasing demands of the ivory trade and big game trophy hunting enthusiasm, elephants, both Asian (*Elephas maximus*) and African (*Loxodonta africana*), often found themselves under the deadly aim of rifles (Rothfels, 2017). Many accounts feature Asian elephants from Sri Lanka. Dixon (1896) retells the tracking of this species, shooting one down and startling the herd, an adult male returned and touched the dead body with its trunk, inspected the bullet wounds in its head, and with its tusks attempted unsuccessfully to raise it upwards, seeming to “realize that its follower was dead” it lifted its trunk and charged the hunters with a scream. Also, Ferguson (1883) was in a party, armed with spears and nooses, set out to capture live wild elephants and found a herd of twelve (an adult male and female, five adolescents followed by three juveniles and two calves). When the rope was tied to one of the calves and it gave out screams the mother was so distressed, that she collapsed and lay panting for an hour until she finally died, the calf would not leave her vicinity and the remaining herd members attempted to lift her body; one such a scene in this location was captured by a photograph (see image). Ferguson additionally recounts the day before an adult female had been shot dead, and two adult members "made a persistent endeavor to raise" her while its calf attempted to suckle from her. Relating to captive females Mubarak (1873) states they mourn their calves, often refraining from eating and drinking and at times "even die from grief". A scene set in 1845 Puttalam, Sri Lanka, relates how two captured elephants died and were left in the makeshift enclosure. A few days after the enclosure was discovered empty: the bodies had been carried outside noting that no creature except a living elephant could have endured their weight (Tennent, 1859). Elephants also share close phylogeny with hyraxes and sirenians. One of the earliest accounts from the 16th century involves the monogamous and now extinct Steller sea cow (*Hydrodamalis gigas*). On a scientific expedition to the Bering sea, Georg Steller described how during the slaughter of an adult female sea cow, her mate tried to defend her unsuccessfully and returned to shore for two days to where her dead body lay (Steller, 1751).

Rodents also surface in this kind of literature. Narrating the story of his guinea pig (*Cavia porcellus*) pet couple, Stillman (1900) describes how the male injured after a fight with a rat, lingered for two or three days until finally expiring. The news came through the wailing of its female who, sounding like a crying child vocalized the whole night, and only in the morning did they find the dead male with its mate wailing next to him. Refusing to be parted with the male and despite having food around her, the female refused to eat and died of starvation two days later. Goodrich (1845) writes about two young North American beavers (*Castor canadensis*) captured alive and taken to a factory near Hudson's Bay where they were kept as pets. When one of the pair was accidentally killed, the other "began to moan" and refused to eat until finally dying from "grief for the loss of his companion". This story is recounted once again by Francis (1881) who adds another case in which the pair were kept together and when one died, the other brought it food appearing not to understand the situation, then finally sensing it would not move, covered its body with twigs and leaves and "pined away", losing its appetite for quite some time. Another anecdote from a German naturalist possibly relating to the Eurasian beaver (*Castor fiber*) states that a beaver approaching a hat made of beaver skin wept over it, soon followed by a female that began to cry "more piteously", ending in the rest of younger beavers attracted by the sound joining in the chorus, suggesting they recognized the hat as belonging to one of their species (Anonymous, 1845).

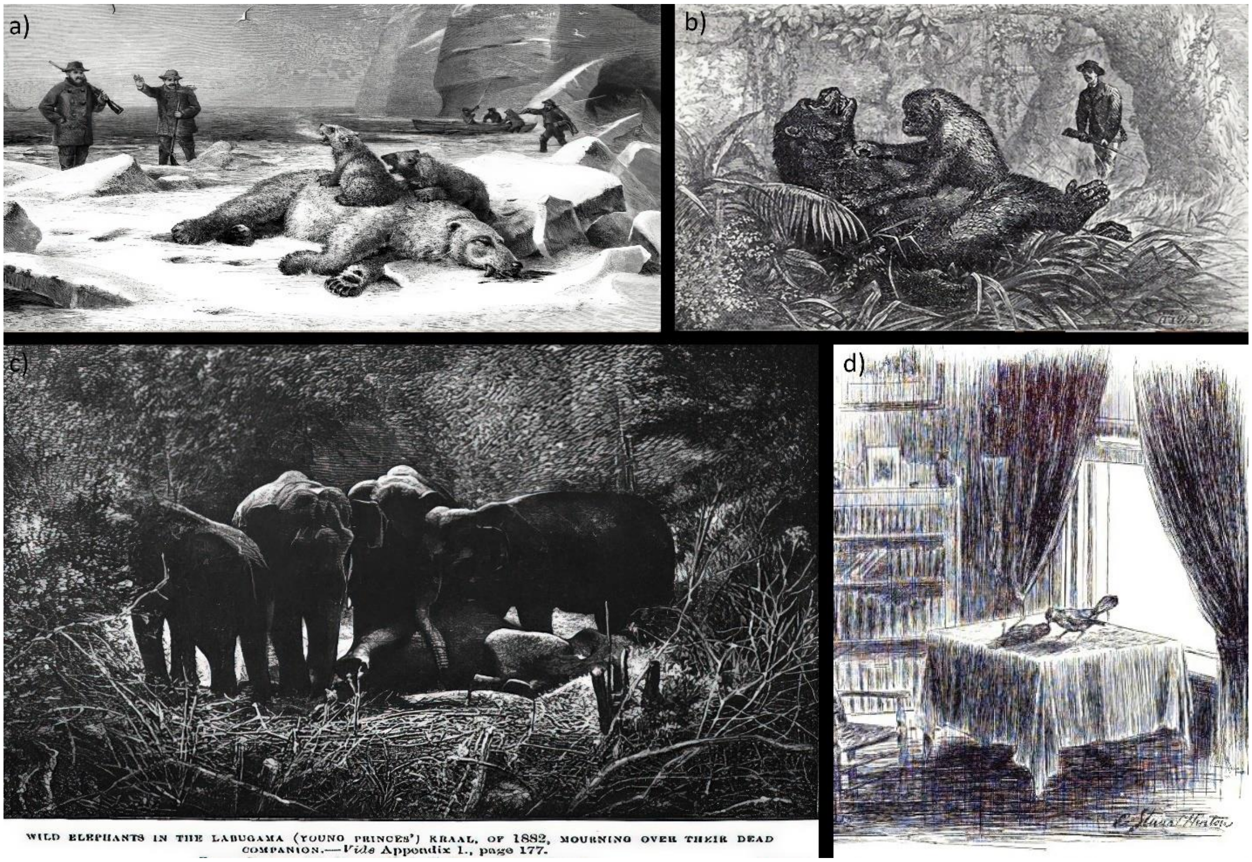

Figure 2.1. Several depictions of interactions with dead conspecifics a) from a bear hunt (Coomstock, 1829) and b) a gorilla hunt (du Chaillu, 1869), d) a bird's mate accidental death (Elliot, 1883) and c) possibly depicting the earliest know picture of elephants in Sri Lanka interacting with their dead group member (Ferguson, 1884). All images are in the public domain.

## 3. Early Descriptions on Mammals II: Non-human primates

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*, Frederic 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). While traveling 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). Arthur Brown (1879) published a report on a captive male chimpanzee's (Pan troglodytes) behavior following the death of its female 'cagemate' – attempting to rouse the corpse, crying, and then whimpering. Richard Garner, in his endeavor 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). The first depiction of dead infant carrying comes from a depiction of lowland gorilla behavior by the English traveler Thomas Bowdich who retells from his interviews with slaves and merchants, while aboard a ship heading towards Gabon, how the females of the species were observed carrying their deceased infants until they decomposed (Bowdich, 1819).

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 behaviors towards their dead: (i) carrying/dragging corpses (Bowdich, 1819; Mollien, 1820; Kipling, 1891; Loveridge, 1923); (ii) mobbing/defending corpses from attackers (Forbes, 1813; Johnston, 1885; Jenks, 1911; Reichenow, 1920; Aschemeier, 1921); and (iii) 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 behavioral patterns that are recurrent in present-day observations.

# Section 2. Evolutionary approaches to comparative thanatology

# Chapter 3. Comparative thanatology of Vertebrates[3]

## 1. Detecting life

### a) Evolutionary landmarks

Before addressing the question of how animals detect death, it is noteworthy to consider, generally speaking, how they detect life and the mechanisms behind such capacities. Animals, in their natural environments, are confronted constantly with dynamic visual signals. Accurate interpretation of these signals is a significant factor for evolutionary fitness as they can both come from either living entities (self-propelled motion patterns) or non-living entities (objects moved only by external forces) (Thurman & Lu, 2013). This capacity to differentiate biological from non-biological movement is part of an ancient mechanism evolved for modulating interactions with other organisms, whether they be predators or prey or conspecifics (kin, mates, and other social partners or competitors).

This movement expressed through self-propelled motion was arguably existing in the first living organisms during the Pre-Cambrian Period some 3000 Mya. Just as unicellular organisms today, they likely moved about with the aid of cilia and flagella (hair-like structures assisting the motion) (Wolpert, 2003). As with today, predation was already a strong selective force, one of the strongest factors that gave rise to eukaryotes (multi-cellular organisms) (Davidof & Yurkevitch, 2009) at around 1600-2500 Mya (Knoll, 2015). During the Ediacaran Period (635-540 Mya), it is believed the first *metazoans* (animals) arouse[4] (Sebé-Pedros et al., 2017), that would later diverge

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[3] A version of this chapter has been published in: Gonçalves, A., & Biro, D. (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), 20170263.

[4] See, however, estimates based on molecular clock data suggesting that the metazoan nervous system originated much earlier, in the Cryogenian (850–635 Ma) (Wray, 2017).

into chordates, mollusks, and arthropods, as indicated by the genetic data and fossil record (Erwin et al., 2011). Metazoan life in these environments was essentially two-dimensional and confined by bio-mat grazing (Gingras et al., 2011). All these interactions were made possible by an incipient evolution of vision starting in unicellular organisms possessing photo-receptor cells to multicellular organisms capable of navigating by discerning between light and darkness. From *eye-spots* in both early prokaryotes to metazoans that engaged in *phototaxis* (movement towards light), to *prototypical eyes* capable of discerning shape and movement to more *complex eyes* (compound and camera-type) were then subjected to divergence, convergence, and parallel evolution (Gehring, 2014). Fast-forwarding to the Cambrian Period (541-485 Mya), the animate environment perceptually becomes, even more, three-dimensional (Holland, 2015), we have already biological innovations that would persist to the present day; nervous systems and brains (Northcutt, 2012), attentional states (Grazianno, 2014), associative learning (Ginsburg & Jablonka, 2010), embodied cognition (Trestman, 2013) and the initial stages of primary consciousness, supposedly formed by the evolution of *camera-type eyes* (Feinberg & Mallatt, 2013).

## b) Perceptual life detectors: EMDs and Biological Motion

Vision is the culmination of numerous computation processes that begin in the retina and, arriving first in the cortex in the *primary visual area*, conclude by spreading out through several other cortical spaces. Except for some teleost fishes, brain complexity among vertebrates generally follows a more-or-less predictable pattern in the phylogenetic tree. Next to agnathans (lampreys and hagfish), amphibians (frogs and salamanders) possess the lowest levels of brain complexity being regarded as being highly instinct bound whereas reptiles (turtles, lizards, and snakes) have brain anatomy distinctly more complex in comparison. They are followed by birds and mammals who exhibit the highest complexity, together while some teleost fish taxa (cichlids) also exhibit signs of complex behavior and intelligence (Roth, 2015). All these taxa share a common ancestor from the Cambrian period that, like them, possessed a camera-type eye which led to improvements in locomotion, food-seeking and handling, predation and predator avoidance, and primary consciousness (Feinberg & Mallat, 2013). Despite many animals lacking the capacity to detect color or have binocular vision, apart from the ability to detect light and dark, motion detection is likely one of the oldest and more elementary visual abilities (Nakayama, 1985).

In their seminal research on fly optics more than a century ago, Cajal & Sanchez (1915) were already making analogies to the vertebrate retina. So deep is this homology in part, that even modern metazoan phyla as separate as mammals and insects share some of the same genes controlling eye formation (Gehring, 2005). Today we do know there are striking parallels between insect and mammalian visual systems, studies have shown they share similar extracting motion information via parallel ON-OFF neuronal pathways, the motion detection involves a correlation of signals with distinct temporal dynamics, and the primary motion information from both pathways converges which results in four groups of neurons that are selective for right-left up-down directions. Such parallels, either derived from a common urbilaterian ancestor or the product of convergent evolution, do represent a "robust solution" to computing the direction of motion with visual neurons (Borst & Helmstaedter, 2015).

A theoretical model created to explain these minimal computations essential to perceive movement from the activation of photoreceptors was developed in the 1950s by Berhard Hassenstein and Werner Reichardt. It is now referred to as the Hassenstein-Reichardt EMD or simply the EMD (Elementary motion detector) in which the eye maps an image of the world into a sheet of photoreceptors. Comparative research done since has been shown to obey this model;

movements in the environment are extracted by these neural circuits comprising motion detection and reacting to temporal local shifts of image intensity on the retina (Frye, 2015). Examples of these computations are found in vertebrate species such as frogs, lizards, and fishes below that react accordingly even if the perceived movement originates from artificial stimuli.

Frogs can make simple operations in their environment, they are able to distinguish moving prey of distinct sizes (Anderson, 1993). Early neurological research found that frogs react strongly to the movements of small dark spots that triggered a feeding response in frogs. Certain retinal ganglion neurons they believed were at the cause of this perceptual response and termed them *bug detectors* (Lettvin et al., 1959). As frogs did not evolve to detect non-moving small objects, even if they are placed with dead insects which are equally as nutritious as live ones, they will starve to death (Roth, 1986). Anoline lizard species are known to communicate visually with displays of head and body motions. Males often engage in so-called *assertion displays* believed to attract females and repel other males (Fleishman, 1992). And these signals have to be detected even if occasionally there is competing environmental motion. In an experiment, when lizards were presented with artificial stimuli mimicking display movements, it was detected by the lizard both in settings with and without moving vegetation; even with background distractors (leaves moving via force of the wind) they accurately detected the appropriate biological moving signals (Fleishman & Pallus, 2010). Zebrafish, like many teleost fishes, exhibit *shoaling behavior*, a collective behavior that enables predator avoidance, foraging, and stress coping, the onset of which begins at two weeks of age (Pritchard et al., 2001). When presented with circular black dots projected onto a screen and exhibiting the kinetics of zebrafish bouts, juvenile naïve zebrafish will match these movements triggering a shoaling response in them (Larsch & Baier, 2018).

These examples in the three taxa share one common thread; their behavior is triggered by the perception of *biological motion*, presumably via *elementary motion detectors* whether such stimuli signals prey, competitors, or social partners. The research into biological motion began 40 decades ago with humans (Johansson, 1973). When presented with stimuli consisting of moving point-light displays against a contrasting background depicting a moving human, despite being severely impoverished percepts, the visual system decodes these point-light displays when their movement corresponds to the typical semi-rigid biological motion but not when their movements depict non-biological motion. This is also true for other species; newly hatched chicks, when presented with a set of moving dot-stimuli representing a conspecific versus a set of moving but scrambled or inverted dot-stimuli will look for longer durations at the regular conspecific moving dot-stimuli (Vallortigara & Regolin, 2006; Mascalzoni et al., 2010). This innate response has also been attested in humans (Simion et al., 2008; Bardi et al., 2011). In fact, biological motion detection has been termed as evidentiary for a *perceptual life detector* common to vertebrates (Johnson, 2006). Additional studies with other species support this hypothesis of an ancient neural mechanism for the detection of *animacy* in species such as teleost fishes (Nakayasu & Wakanabe, 2014; Schluessel et al., 2015), rats (McKinnon et al., 2010), cats (Blake, 1993), pigeons (Troje & Aust, 2013), dolphins (Herman et al., 1990) and non-human primate species such as common marmosets (Brown et al., 2010), rhesus macaques (Oram & Perrett, 1996), baboons (Parron et al., 2007), and chimpanzees (Tomonaga, 2001) attending preferentially to *biological motion* stimuli.

In humans, according to neuroimaging studies, biological motion processing involves specialized cortical areas, notably the *posterior superior temporal sulcus* (pSTS) (Grossman & Blake, 2001; Vaina et al., 2001) and additionally, the *fusiform body area* (FBA) (Jastorff & Orban, 2009). Despite a 25 million-year divergence with humans, rhesus macaques[5] also show the activation of homologue brain regions, such as their *superior temporal sulcus* (STS) upon viewing biological motion point-light displays of conspecifics (Jastorff et al., 2012).

The perception of biological (dynamic) cues is but one of many components of a larger perceptual neural system for animacy detection that comprises *detectors* of other biological (featural) cues such as faces, eyes, and particular animate shapes (Parr, 2011), with other sensory modalities in such as sounds, odors, and textures being fundamentally tied with agency detection and attribution for *animate entities* (*sensu* Ghazanfar & Santos, 2004). Biological movement, by and large, does present a robust cue for another important categorical distinction; *animate* versus *inanimate entities*. Indeed, studies with 12-month-old infants show that biological movement, contrary to non-biological movement, is a critical feature that primes for attribution of animacy (Poulin-Dubois et al., 2015).

## c) The animate/inanimate distinction

*"[Of the proper subjects of motion some are moved by themselves and others by something not themselves, and some have a movement natural to themselves and others have a movement forced upon them which is not natural to them. Thus the self-moved has a natural motion. Take, for instance, any animal: the animal moves itself, and we call every movement natural, the principle of which is internal to the body in motion (...)"*

Aristotle [circa 350 B.C.E., *Physics, vol. V, p. 307)*]

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[5] Macaque brains are repeatedly described as suitable models for the human brain, while there is some truth to this claim, it is at the same time misleading, since macaques reflect independent evolution over the course of millions of years, based on general commonalities alone, they should not be taken *prima facie* as miniaturized versions of the human brains, since often human brain regions do not necessarily possess their non-human brain homologues (Passingham, 2009). These comparative studies above do, however, give strong credence to a shared function given the anatomical position and similarities of the brain structures paired with their neuronal activation for the same sets of stimuli.

*The tendency in savages to imagine that natural objects and agencies are animated by spiritual or living essences, is perhaps illustrated by a little fact which I once noticed: my dog, a full-grown and very sensible animal, was lying on the lawn during a hot and still day; but at a little distance a slight breeze occasionally moved an open parasol (...) every time that the parasol slightly moved, the dog growled fiercely and barked. He must, I think, have reasoned to himself in a rapid and unconscious manner, that movement without any apparent cause indicated the presence of some strange living agent and no stranger had the right to be in his territory."*

Charles Darwin [1871., *The Descent of Man, p. 67)*]

Perception of animacy[6] (i.e. detection of biological motion with animate shapes) is intrinsically tied with *dynamic cues* such as *goal-directed movement* (the orientation to which an agent moves to a perceived objective) and *contingency of behavior* (the timing amongst an agent's actions and specific events) (Opfer & Gelman, 2011) but also *featural cues* such as body parts (faces, eyes, bodies, textures) (Rakison & Poulin-Dubois, 2001). Most studies done in this area involve humans, measuring their abilities to detect and decipher an agent's intentions. In a very famous example, the *change detection paradigm*, humans show preferential processing of inanimate over inanimate stimuli; not only do they capture attention quicker, but animate stimuli is also better remembered in detriment to inanimate stimuli (Nairne et al., 2007; New et al., 2007; Altman et al., 2016). The underlying rationale for this appears to result from evolutionary adapted mechanisms tied to the need to monitor *agents* over *non-agents* since they are more crucial to survival and fitness. Studies with pre-linguistic infants show us very early on, they can distinguish between living and non-living entities (Premack, 1990; Woodward et al., 1993; Spelke et al., 1995).

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[6] Often conflated with each other, *animacy* and *agency* merit some distinction here. The *animacy* concept is comprised of both *dynamic* and *featural/static* cues to life often but not restricted to visual perception (i.e. typically behaving animals), while *agency* pertains only to the dynamic cues (i.e. goal directed/contingent movement). For instance, *agency* can be decoupled experimentally from *animacy* in the lab through moving inanimate objects that have little or no *featural* characteristics of animacy. It follows logically that these constructs are processed by distinct areas in the brain, as neuroimaging research in humans suggests (Gobbini et al., 2011).

Infants also imbue agents and agent-like entities with intentionality as shown in the seminal experiments by Amanda Woodward using the *habituation-dishabituation paradigm*. In these, when infants see a human hand reaching for a particular object, they react to changes in its goals, whereas no such response is observed when a mechanical rod/claw is used in place of the hand; when a human reached for an unexpected object they looked longer at this incongruent action, something they did not when a claw/rod exhibited the same actions (Woodward, 1998; Woodward, 1999; Woodward et al., 2001; Daum & Gredebäck, 2011). This is supported by other experiments that show infants 5-9 months are unable to reason about the goals of computer-animated events showing “inanimate agents” when they interact with other “inanimate agents” (Csibra et al., 1999; Csibra et al., 2003; Kuhlmeier et al., 2003). However, when presented with simpler events, for instance, a single box moving towards either a cylinder or a cone, 3 to 5-month-old infants appear to attribute intentionality to them (Luo & Baillargeon, 2005; Luo, 2011). This suggests that while agents (i.e. humans) are a robust cue for attributing intentionality, “inanimate agents” exhibiting certain life-like features, such as self-propelled motion, may also trigger intentional/goal attributions.

Neuroimaging research also shows that distinct regions in the brain are related to processing animate compared to inanimate entities (Caramazza & Shelton, 1998; Grossman et al., 2002; Morito et al., 2009; Wigget et al., 2009). For instance, Caramazza and Shelton (1998) were among the earlier modern researchers arguing for an evolutionarily adapted domain-specific knowledge system for animate and inanimate entities that are subserved by distinct neural mechanisms, a position strengthened by experiments with brain-damaged patients that showed impairment in recognizing and naming animate entities. More recently, Wiggett et al. (2009) found specific visual brain regions (ventrolateral) were activated during processing several animate stimuli whereas other regions (ventromedial) were activated during processing several inanimate stimuli.

While the animate-inanimate distinction appears to be a conserved mechanism and manifested in most animal lineages, particularly vertebrates (a contrary hypothesis seeming untenable), experimental evidence for such is rather lacking, involving non-human animals such as rodents, canids, and primates. Analogous variations of Woodward's reaching experiments show that both capuchin monkeys (Phillips et al., 2009) and rhesus macaques (Wood et al., 2008) make a distinction between objects reached by humans *versus* inanimate objects. For instance, Wood and colleagues found that rhesus macaques would inspect the coconut (out of two coconut choices) that the human experimenter previously inspected with his hand or foot but not when he used objects (pliers, poles, machete), which according to the authors, were actions that fell outside their motor repertoire, thus they made no intentional attributions. Moreover, Phillips and colleagues found that when capuchin monkeys were presented with food by an unwilling, versus an unable human experimenter, they left the experimental booth sooner in the unwilling situation, however when these actions were performed by a willing *versus* unwilling stick they showed no such difference. What the results show is that the subjects were correctly attributing intentions towards agents (even in conditions when only human hands were visible) but not to inanimate entities.

Dogs have also been tested using variations in Woodward's experiment. Marshal-Pescini and colleagues (2014) presented dogs with humans interacting with one of two objects, even when object positions were switched, the dogs looked longer at new object-directed goals rather than the same object but with switched side. No such difference was found when a black box was doing these movements instead of a human agent which suggests that, unlike an "animate agent" (human), they do not perceive an "inanimate agent" (box) actions as goal-directed. But while the “inanimate agent” exhibiting *dynamic cues* to animacy can be judged more or less as not goal-directed in some of these experiments, consequently, the more it exhibits featural cues to animacy the more it will be judged as goal-directed: thus an agent. Kupferberg and colleagues (2013), using common marmosets echo the same results as other Woodward-type experiments, having been habituated with videos of conspecifics interacting with object A and not object B when presented with videos of conspecifics reaching object B and not A, they looked longer. The same pattern was shown when observing humans performing the same actions, but not a moving black box, however, when observing videos of a monkey-like robot exhibiting the same reaching behaviors towards one of the objects, the marmosets again, as with the conspecifics and humans, looked longer when it reached for a new object. Not unlike Darwin’s dog, the movement of inanimate entities can cause specific responses in wild jackdaws. Greggor et al., (2018) found that these birds were startled by movement irrespective of whether the stimuli were animate (fake snake, mounted birds) or inanimate (sticks/branches) but whereas they produced more alarm calls with the animate stimuli, they delayed the longest entering their nests which, according to the authors suggests they recognized the event as unexpected, scanning it for longer durations.

As with humans, the animate and inanimate entities as conceptual categories in other animals may relate to distinct neural circuits representing evolutionarily adaptive domain-specific knowledge systems. Neuroimaging studies, again, in macaques, presenting color images of animate and inanimate entities (faces/body parts vs objects/landscapes) show neuronal activation for inanimates in the temporal cortex and the intraparietal sulcus. No distinct organization was found in the visual cortex areas V1-3, but there was an animate-inanimate division in V4 (Pelekanos et al, 2017). Previous studies in the same macaque species, comparing it to humans, using the same methods, show the *inferior temporal cortex* (IT) forms category clusters corresponding to animate and inanimate entities; in the animate entities, faces/bodies have more specific regions dedicated for each animate part (they form subclusters in the IT) and the inanimate data suggests a more linear separability between animates and inanimates in the IT but not the early visual cortex. This brain region is considered to contain high-level representation of visual information at the perception-cognition interface (Kiani et al., 2007; Kriegeskorte et al., 2008).

## 2. Detecting death

### a) Landscapes of fear and disgust: necrophobia

Unlike detecting for life, detecting death-related stimuli, at first glance, presents no clear or immediate adaptive value. But corpses can be a useful source of information; they can *signal*[7] danger (i.e., a predation event, or a pathogen hazard), they can be a source of food, or, in the case of social animals they can signal changes in the hierarchy (Gonçalves & Biro, 2018; Gonçalves & Carvalho, 2019). Among vertebrates, scent-cues to death such as *cadaverine* or *putrescine*, alongside other decay-related substances (hydrogen sulfite, methane, and ammonia), will typically elicit aversive responses. This has been shown in rodents, including various species of mice, voles, shrews, and chipmunks, also avoid areas where deceased rodents—even heterospecifics—are present, presumably at least partly informed by olfactory cues associated with decaying flesh (Prounis & Shields, 2013). California sea lions reportedly avoided a pool used for cooling after the carcass of a dead pup fell into it, moving away after apparently sniffing at it (Peterson & Bartholomew, 1967).

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[7] Here I use the word *signal* in the broadest sense. In contrast, authors such as Bonnie and Earley (2007) make the distinction between *signal* and *cue* with regards to intent of communication. While both definitions may carry useful information to the receiver, signals (intentional) are traits selective for their communicative purposes while *cues* (unintentional) are by-products of form, behavior, and physiology and, unlike *signals*, not necessarily dependent upon a receiver (real or perceived). According to the authors, these probably can be acquired through trial-and-error, although there's also an argument to be made on aspects pertaining to their innate character.

Not only in terrestrial surroundings this also holds for aquatic environments. Zebrafish show elevated stress levels upon detecting cadaverine (Oliveira et al., 2014) and actively avoiding it (Hussain et al., 2013). Moreover, phylogenetically distant taxa such as sea lampreys (Bals & Wagner, 2012) and sharks (Hart & Collin, 2015) have been recorded to avoid *conspecific necromones* (odors emanating from the decaying tissue of a conspecific). Moreover, when exposed to *conspecific necromones,* juvenile Port Jackson sharks (*Heterodontus portusjacksoni*) reduced their oxygen uptake rate up to 3 hours, a reaction analogous to fear-induced bradycardia or freezing behavior, suggesting *necromones* trigger anti-predator response (Gervais & Brown, 2021).

In humans, a range of interesting emotional and conscious, and unconscious responses to putrescine have been documented, including increased vigilance, active and planned retreat, and hostility towards out-group members (Wisman & Shrira, 2015). While a replication study did find similar aversion responses to putrescine, hostility towards out-group members was not found (Anes et al., 2020). Captive chimpanzees also show an aversion to putrescine: when this odor was paired together with objects (a stuffed glove or a dead bird), chimpanzees spent significantly less time near it regardless of the object type in comparison to when the same object was paired with other substances (such as ammonia or water) (Anderson et al., 2021). However, not all vertebrates show avoidance: in rats, cadaverine and putrescine elicit the burying of dead conspecifics and other objects (Pinel et al., 1981), and in goldfish, the same chemicals enhance feeding activity (Rolen et al., 2003).

### b) Beyond scent: visual, tactile, multi-modal cues

Many animal species exhibit complex responses towards their dead that are not necessarily triggered by scent; furthermore, these often rely on a combination of several sensory modalities.

Here, I explore non-olfactory and multi-modal cue use in corvids, proboscids, cetaceans, and primates, with a focus on observational and experimental field studies. The species comprising these taxa display many complex behaviours across both the physical and social domains and have been argued to possess episodic-like memory. Many live in hierarchy-based social structures in which they cross-modally recognize individuals and act based on their past interactions (Clayton & Emery, 2007; Bates et al., 2008; Marino et al., 2007; Byrne et al., 2009; Veit & Nieder, 2013; Kondo et al., 2012; Seyfarth & Cheney, 2015). Moreover, some individuals in these taxa are able to recognize themselves in the mirror, suggesting self-awareness (Gallup, 1970; Reiss & Marino, 2001; Plotnik et al., 2006; Prior et al., 2008). It has been suggested that such species might be capable of an understanding of death (Byrne, 2016); however, (whatever such understanding entails), there appears to be no qualitative difference between species that fail and those that pass the mirror test of self-recognition in regard to general thanatological behavior (i.e. dead infant carrying, exploratory behaviors towards the corpse, vigils, visitations, etc.) (Gonçalves & Carvalho, 2019).

### (i) Corvids

The family Corvidae includes crows, ravens, rooks, magpies, jays and jackdaws. These species generally live in bonded pairs, possess the largest relative brain size of any avian group and show rates of behavioral innovation and complexity unparalleled in other bird species (Taylor, 2014).

Observations of thanatological behaviors have been made in several corvid species. Several reports describe *ceremonial gatherings* or *cacophonous aggregations*: an assembly of live birds near a deceased conspecific. The participants utter alarm calls but seldom touch the corpse or show aggression, in comparison to their predator mobbing or scavenging the corpse of another species

(Heinrich, 1999; Marzluff & Angell, 2012; Bekoff, 2007; Miller & Brigham, 1988; Pierotti & Annett, 2014). Also, compared to the amount of time spent by cetaceans, elephants and primates near corpses (see below), these gatherings tend to be relatively short-lived. There are reports of objects (feathers, sticks/grass) being placed near the corpse (Bekoff, 2007; Marzluff & Angell, 2012). Survivors subsequently tend to avoid the place where a dead conspecific is found (Swift & Marzluff, 2015), so much so that effigies have been found useful for pest control (Avery et al., 2008; Peterson & Colwell, 2014).

In many bird species, a dead conspecific generates cautious inspection and/or mobbing behaviors (reviewed in Curio, 1993). Lorenz (1952) reported his tame jackdaws (Corvus monedula) attacking him when he carried his black swimming shorts in his hand, and suggested that the likeness of the trunks to a dead jackdaw triggered this mobbing behavior. Barash (1972) paired a predator model—a great horned owl (*Bubo virginiatus*)—with either a black cloth or a crow model and obtained similar results: live crows (*Corvus brachyrhynchus*) mobbed these significantly more than the owl model alone. Feathers resembling those of a conspecific may also trigger alarm responses in several crow species (Lorenz, 1971; Verbeek, 1972; Kilham, 1982). The primary mode of recognition, therefore, is likely visual: corpses not exhibiting visual cues such as colored feathers will not elicit responses from live conspecifics. For instance, Heinrich (1999) described how a dead crow he attempted to feed to live ravens (*Corvus corax*) was promptly rejected; it was only accepted as food after removal of the feathers, head, wings and feet. Similarly, Lorenz (1971) found that adult jackdaws did not mob him if he was holding a young jackdaw before it acquired black feathers, but they did after those feathers grew. In what can be termed the *information-gathering hypothesis* (Anderson, 2016), assemblages around a dead conspecific might serve to acquire information surrounding the death and to assess a potentially dangerous situation.

Additionally, assembling corvids might be appraising new social changes in the group [Marzluff & Angell, 2012; Miller & Brigham, 1988; Swift & Marzluff, 2015; Curio, 1993; Iglesias et al., 2012). Three experiments formally tested these hypotheses [Swift & Marzluff, 2015; Iglesias et al., 2012; Iglesias et al., 2014). In scrub-jays (*Aphelocoma californica*), corpses of conspecifics and similar-sized heterospecifics elicit aggregations and site avoidance (Iglesias et al., 2014). A corpse in prone posture elicits cacophonous aggregations, whereas an upright one elicits mobbing behavior (Iglesias et al., 2012). (see also Swift & Marzluff 2018). Moreover, unlike dead conspecifics, corpses of pigeons (*Columba livia*) elicit little reaction in crows. Interestingly, pigeons are similarly low responsive to dead pigeons, suggesting that this species processes and evaluates the situation differently from crows (Swift & Marzluff, 2015). Earlier research on wood pigeons (*Columba palumbus*) used models and showed that pigeons tend to avoid corpses of conspecifics as a default response (Inglis & Isaacson 1984; 1987), which contrasts with corvids' initial curiosity.

Studies on crows have not yet explored how the social relationship with the dead affects the interactions of the living, particularly in the case of pair-bonding corvids, although this has been alluded to in single-case reports (Marzluff & Angell, 2012; Pierroti & Annett, 2014). In addition, compared to the taxa discussed next, corvids show limited prosocial tendencies (Lambert et al., 2017), including little regard for conspecifics beyond kin or mate; this may explain their shorter-duration and more frequently agonistic responses to corpses compared to non-human primates, proboscids and cetaceans.

### (ii) Proboscids

The order Proboscidea comprises three extant species, the Asian elephant (*Elephas maximus*) and the African bush (*Loxodonta africana*) and forest elephants (*Loxodonta cyclopis*). Wild elephants live in complex fission–fusion societies with female matrilineal kin forming a family unit with close, lifetime bonds. The encephalization quotient of elephants rivals that of primates, and they possess as many cortical neurons as humans do, albeit less densely packed than in primate brains (reviewed in Hart et al., 2008; Byrne et al., 2009).

Like non-human primates, elephants have been observed to surround a dead conspecific, interact directly with it, touch it with their feet or trunks, at times attempt to lift it with either foot or tusks, and vocalize in apparent distress. They may also guard the body against predators or other conspecifics and revisit the corpse in the following days (Moss, 1988; Poole, 1996; Payne, 2003; Douglas-Hamilton et al., 2006). Adult females have also been observed carrying dead infants weeks after death (Bere, 1966; Sikes, 1971; Douglas-Hamilton & Douglas-Hamilton, 1975; Sharma et al., 2020). Unlike non-human primates observed to date (but see Boesch, 2012), elephants occasionally cover dead conspecifics with branches, leaves or soil, and may attempt to patch wounds on the dead with dirt or place food in their mouths (Harthoorn, 1970; Sykes, 1971; Douglas-Hamilton & Douglas-Hamilton, 1975; Moss, 1988; Buss, 1990; Moss, 1992). It is important to consider these behaviors in the context of the elephant's social repertoire with live conspecifics and heterospecifics. Elephants have reportedly buried humans and other dead animals (Melland, 1938; Grzimek, 1956). Presumably, as with chimpanzees at Tai, it could be done to elicit a response from the dead individual (Boesch, 2012). Alternatively, it could represent something of a cultural tradition present in some African elephant populations and not in others, that might have been in place for millennia and as such, with dwindling wild elephant populations, subjected to potential loss. The earliest known account comes from the third century A.D. via Claudius

Aelianus (Aelian, 2011). Caitlin O’Connell (2020) describes the case at the Fresno Chaffee Zoo in California: after the matriarch died, the zoo keepers allowed her body to be viewed by the remaining group members, and two females (particularly close to her in life), stayed with the body for extended periods, occasionally sprinkling dirt at her body. By morning, her body was covered by roughly “a quarter of an inch of dirt”. Interestingly these two females were wild born, having been brought over from Mozambique at around 6 and 7 years of age. O’Connell raises the possibility that they might have witnessed similar behaviors in the wild. No other elephants at this Zoo had been observed engaging in this behavior, and unlike the two females, the rest were all captive born.

Contact behaviors with the corpse include using the trunk to inspect the head and body; even the torso may be used for such inspections. Pulling and stepping over the corpse have been observed, as have scent-related behaviors such as sniffing the corpse with the tip of the trunk and displaying the flehmen response (touching the tip of the trunk to the openings of the vomeronasal organ). Elephants may also put the trunk in their mouths to assess gustatory information about the corpse (Douglas-Hamilton et al., 2006; Merte et al., 2008). Elephants show striking responses to the bones of other elephants, particularly skulls and tusks, carefully inspecting them (Douglas-Hamilton & Douglas-Hamilton, 1975; Moss, 1992; Spinage, 1994). McComb et al. (2006) showed experimentally that African elephants are primarily attracted to tusks in comparison to skulls, pay more attention to conspecific skulls than other objects, and show no evidence of recognizing the skulls of familiar conspecifics. The attraction to tusks might be because they represent an externally visible cue to identity that is consistent across life and death.

Playback of calls of dead elephants to live group members have also been attempted (McComb et al., 2000). When vocalizations of a female were broadcast to her family unit 3 and 23 months after she had died, group members responded with contact calls each time, even approaching the speaker (but did not do so in control trials involving the vocalizations of unfamiliar individuals), suggesting long-term memory and recognition. As it was not specified whether the group members had directly observed the death or seen the female's corpse, it is unknown whether responses to playback calls would differ depending on such knowledge (for a similar case, see also O'Connell, 2021).

### (iii) Cetaceans

Thanatological behavior among cetaceans (whales, dolphins, and porpoises) is also becoming increasingly well documented and shows many parallels with primate and proboscid data. The vast majority of reports (compiled in Reggente et al., 2018: see also Bearzi et al., 2018, for a recent review) concern interactions with dead calves or juveniles; carrying their carcasses has been documented in various dolphin and whale species. Indeed, the behavior has been observed worldwide and in a range of environments including open oceans, bays and inlets, and rivers (Reggente et al., 2016). Although carrying can be for extended periods, due to the nature of the aquatic environment, rapid decomposition limits carrying duration in comparison to, for example, primates in dry habitats. Carrying typically involves holding the calf on the dorsal fin, against the melon, or in the mouth. Along with transport, potentially breathing-assisting behaviors such as lifting the corpse to the surface of the water and pushing it down have been observed (e.g. Mann & Barnett, 1999; Quintana-Rizzo & Wells, 2016).

Aside from transport, several other categories of behaviors have been documented, including striking the corpse, non-contact attendance such as stationing next to the corpse, and sexual arousal and copulation (towards adults only; e.g. Dudzinski et al., 2003). Unrelated individuals also occasionally interact with corpses, and carriers of an infant corpse are frequently seen surrounded by other pod members swimming in cohesive, possibly protective formations (Reggent et al., 2016)

Like proboscids, cetaceans possess a keen sense of hearing that likely plays an important role in navigating their physical and social environments (Whitehead & Rendell, 2014); however, most cetaceans do not possess a sense of smell or taste (Cozzi et al., 2017). This is likely to impact both the sensory drivers and the nature of their interactions with the dead. Visual cues (presence of wounds, lack of autonomous movement) and lack of auditory cues (vocalizations) are the most probable sources of information about a deceased conspecific's state.

### (iv) Vertebrate species in context

Outside of the taxa discussed above, various mammalian species including rhinoceroses (Williams et al., 2002), hippopotamuses (Inman et al., 2019), giraffes (Kok, 1982; Muller, 2010; Carter, 2011; Strauss & Muller, 2013; Bercovitch, 2012), otters (Kenyon, 1969), dingoes (Appleby et al., 2013), seals and sea lions (Pierrotti & Annett, 2014; Allen, 1980; Rosenfeld, 1983; Lawson & Renouff, 1985; Austin et al., 2001; Pavés et al., 2008), equids (Mendonça et al., 2020; O'Connell, 2020), mooses (Johnson et al., 1973; Sigman & Franzmann, 1978), and manatees (Hartman, 1979; Tennant & Hazelkorn, 2019) have been observed stationing around, manipulating, or carrying their dead infants for extended periods of time. Phylogenetically ancient maternal caretaking mechanisms continue to operate even after the offspring has died in both mammalian and avian taxa. On a proximate level, the mother may perceive the infant's condition as ambiguous, or she may anticipate that the infant will yet recover, whereupon she continues her caregiving. On an ultimate level, her actions likely represent behavioral error because of the cost of too readily abandoning a potentially temporarily unresponsive infant. A transitional phase ensues that can vary widely (days, weeks, or months), during which the mother will carry or stay in close proximity and interact with the corpse (e.g. inspecting, grooming, licking); these responses will decrease over time, culminating in abandonment or occasional consumption of the corpse.

Nonetheless, primates, proboscids, cetaceans, and corvids (to some extent) appear to exhibit the greatest similarities in thanatological behaviors, a trend one predicts to occur in other behaviorally/socially complex taxa (e.g. collared peccaries in de Kort et al., 2018). This is surprising as they do not share a recent evolutionary past and occupy different ecological niches. What they do have in common, however, are complex societies, extended parental care, and large brains.

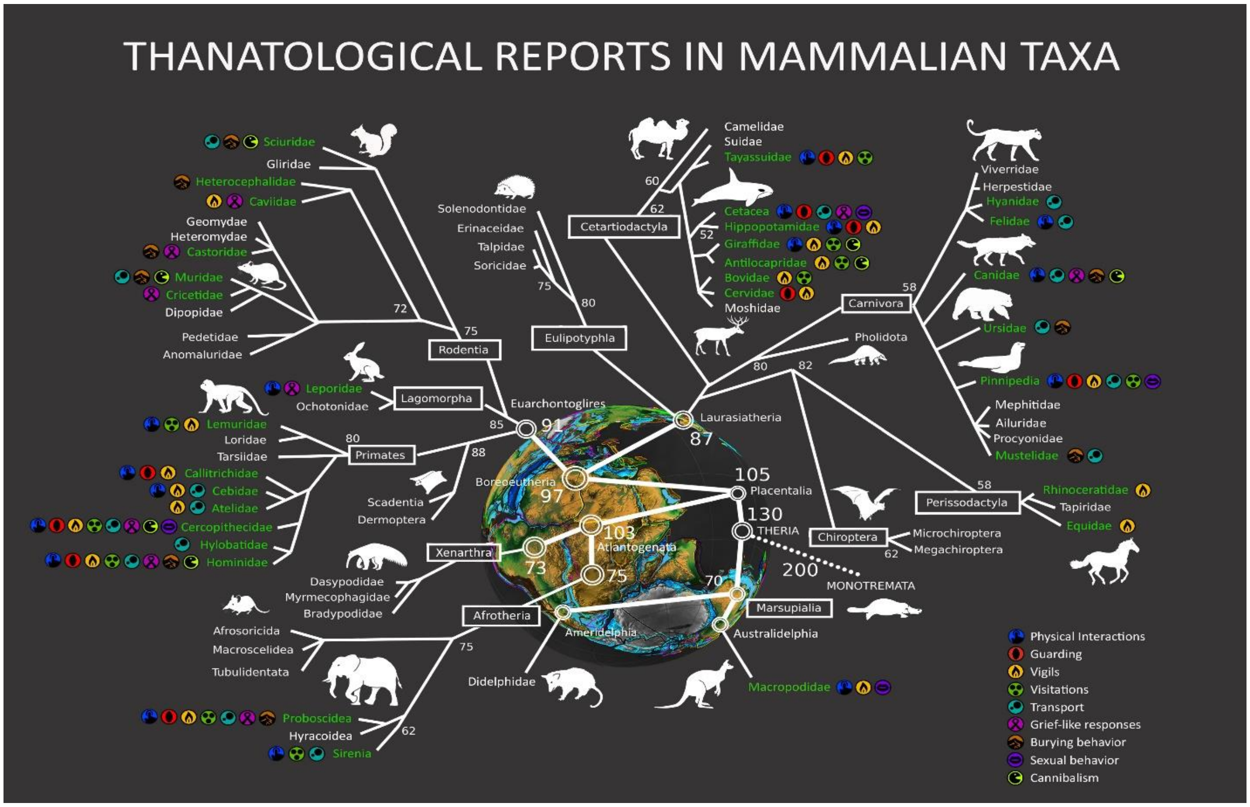

Figure 3.1. Thanatological reports in mammals. Many species display several parallels with each other, namely grief-like responses and secondary thanatological interactions (guarding, vigils, visitations). Phylognetic tree based on Graphodatsky et al. (2011).

Hence, the parallels among these taxa in thanatological responses may be the result of similar perceptual-cognitive processing rules (i.e. sophisticated agency detection) that evolved in the context of increasingly complex social environments. Responses to adult conspecific corpses are both stronger and longer than in other taxa, in which a common response is either avoidance or disregard (e.g. rodents, Prounis & Shields, 2013). Alternatively, the fewer occurrences of thanatological behaviors such as *post-mortem gatherings*, reported in other vertebrate species could be due to observation bias (see also Figure 3.1 for an overview of thanatological responses).

## 3. The 'uncanny' corpse

What are the perceptual-cognitive processing rules that give rise to complex thanatological responses? Here, I draw on several aspects of visually-oriented animals' detection of dead conspecifics to propose a novel synthesis of underlying cognitive mechanisms. Species with larger brains and more advanced cognitive processing, causal reasoning, and information-gathering abilities appear to have comparable responses, suggesting an overlapping phenomenon that is shared across them.

### (a) Threat assessment mechanisms

Brains coupled to nervous systems evolved as a means to process ecologically relevant information and to orchestrate adaptive interactions with the surrounding world. They emerged to deal with the challenges that arise from the physical and social environments, and as these became increasingly complex, so did organisms and their brains (Sol, 2009; Ginsburg & Jablonski, 2010; van Horik & Emery, 2011; Feinberg & Mallat, 2013). Detecting cues to the presence of life-threatening risks remains critical for animals, and natural selection has equipped organisms with and without large brains to do this. However, with associative learning, animals no longer adapted only through evolutionary time, but also within their lifetimes via experience-based behavioral adjustments. Thus, cognition and memory, capacities shaped by natural selection, are critical in regulating expectation, detecting discrepancies, and anticipating events.

The corpse, a highly salient object, represents a conceptual novelty (any familiar object displayed in unfamiliar configurations or unfamiliar settings) (*sensu* Kagan, 2009). Comparative neuroimaging research has revealed that novel stimuli are encoded by the hippocampus (Maren, 2014) and the amygdala (Balterston et al., 2013) and damage to these areas diminishes fear and vigilance to threats (reviewed in Rosen & Donley, 2006). Cross et al. (2013) used positron emission tomography scans to examine cerebral circuitry involved in integrating visual cues into behavioral responses in crows. Crows possess brain regions analogous to the hippocampus and amygdala in mammals that are activated during potentially dangerous situations. The sight of a novel person holding a dead crow activated visual pathways and the hippocampus, while the amygdala was significantly activated by a predator stimulus (a hawk). These patterns of activity were explained as distinct processing activities when gathering novel threat information (person holding a dead crow) versus retrieving past fear information (mounted hawk).

### (b) The uncanny valley

Corpses, as passive entities, defy expectations, provoke emotions and generate various behaviors in the living. Notably, they present a conflicting mixture of presence (odor, wounds, vermin) and absence of cues (movement, sound, body heat). This contradiction is illustrated by the dual approach/avoidance and exploratory/fearful reactions when encountering a dead body. Paying attention towards dead conspecifics is, as previously discussed, evolutionarily relevant because the corpse might provide information about potential predation events or a pathogen hazard.

Furthermore, taking a proximate approach, the living may be responding to novelty in the form of something ‘uncanny’. The uncanny valley phenomenon was originally proposed by roboticist Masahiro Mori (Mori, 1970; Mori & McDorman, 2012) to describe the eerie feeling humans experience upon encountering a human replica, and I propose that it also applies to thanatological responses in non-human animals. Mori used examples such as hand replicas and dead bodies to describe the drop in emotional valence the closer something resembles living specimens of our own species, movement being a key factor in the intensification of eeriness. Cognitive hypotheses posit that an uncanny eliciting stimulus remains in a category boundary or provokes a perceptual mismatch, two explanations that are not necessarily mutually exclusive (Kätsyri et al., 2015) and not necessarily related to cadavers (but see Moosa & Ud-Dean, 2010). An interesting example of this is Goodall’s description of chimpanzees’ fearful and aggressive responses towards physically deformed conspecifics affected by poliomyelitis who moved in unusual ways (Goodall, 1986b). At the ultimate level, an adaptive pathogen-avoidance mechanism could be at play, whereby abruptly acquired physical abnormalities in conspecifics trigger a disgust response in other group members (*sensu* MacDorman & Ishiguro, 2006; MacDorman et al., 2009).

Steckenfinger & Ghazanfar (2009) attempted to test the uncanny valley effect in rhesus macaques and found that both humans and macaques display the same aversion to realistic reconstructions of conspecific faces, particularly, as predicted by Mori, if these were moving (also see for an example of aversion to a ‘moving’—i.e. dragged—corpse among wild chimpanzees, Biro, 2011). This suggests that the mechanism causing uncanny valley-like responses was present already in the common ancestor of Old World monkeys and *Homo sapiens*. Experimental work with human infants suggests that the uncanny valley phenomenon emerges in the first year of life, likely due to perceptual narrowing and learning/differentiation processes (Lewkowitz & Ghazanfar, 2012). Regarding the quality of dynamic cues, research suggests that the more natural movement is, the more likely it is to be accepted by human subjects (suggesting less of an uncanny effect) (Piwek et al., 2014). Some types of stimuli such as androids or corpses likely fail sensory/cognitive scrutiny based on these learning processes, thus triggering an aversive response.

### (c) Animacy detection malfunction

In primates and other vertebrates, life detection is part of a series of core knowledge systems (Spelke & Kinzler, 2007), in this case, the core system of agency (C.S.A.). The core knowledge theory proposes that hard-wired cognitive skills shape mental representations about the world. It remains unclear how many subsystems contribute to agency representation and how they are interrelated; however, some have been unveiled by developmental and comparative cognitive scientists (Spelke & Kinzler, 2007; Santos & Hughes, 2009; Carey, 2009). The animate/inanimate distinction level likely operates through dual core knowledge systems specialized for dealing with animate and inanimate entities: the aforementioned C.S.A. and the core system of object (C.S.O.), respectively.

Contrary to agents, objects are predictable. They are inert, moving only when an external force is applied to them, and as such, they exhibit no contingency or any of the other traits associated with agency: they neither act nor react, but are acted upon by the living agents. Together with my colleagues, I've proposed *animacy detection malfunction* as a cognitive term for the conflicting responses exhibited by vertebrate taxa upon encountering dead conspecifics. The agency system is not perfect but prone to error; however, in terms of its primary purpose (agent detection), it normally functions well. Inspired by earlier views (Hebb, 1946; Mori, 1970; Boyer, 2001), *animacy detection malfunction* is defined as the conflicting cognitive process upon seeing a corpse brought about by perceptual mismatch ultimately causing a violation of expectation. The mismatch stems from the absence of dynamic cues to animacy with the presence of static cues to animacy and is intensified by individual recognition of the dead conspecific. The corpse then has both animate and inanimate attributes, triggering a conflict between the core knowledge system of agency and the core knowledge system of object.

### (d) Death detection mechanism

Humans have long dealt with conflicting stimuli from corpses through cultural mortuary practices that are rooted in the deep hominid past (Pettitt, 2011). Barrett & Behne (2005) argued for the existence of a *death detection mechanism*, that evolved through the course of human evolution, contending that reliable visual cues indicating death, such as fatal disruptions of the body envelope (e.g. decapitation, severe mutilation), were important in the recategorization from ‘living’ to ‘dead’ in humans. This can be illustrated with reference to predator detection accuracy, where failure results in death. The ability to discriminate a live predator (snake, leopard, crocodile) from a dead one allows for the activation of different behavioral decision-making outcomes with implications for survival (Barrett & Behne, 2005).

In a study of grief after the loss of a companion animal, White et al. (2016) found that humans viewing a corpse that exhibited reliable cues for death (i.e. grievous injuries, disruption of the body envelope) displayed less vigilant behavior than when the corpse was intact. What they termed ‘false recognitions’ (incorrect attributions of sight and sound to the deceased) were also more frequent when the corpse was intact. Adopting and expanding on Barrett and Behne’s *death* *detection mechanism*, these authors suggest that natural selection shaped the increase in vigilance behavior whenever a valuable partner was missing and that attending to reliable cues of death was selected for throughout human evolutionary history.

Earlier applications of these assumptions (i.e. uncanniness, bodily disruptions) feature in experiments on fear performed by Hebb. He revealed concealed objects in a box to captive chimpanzees. Among the stimuli were what he called ‘primate objects’, which included a plaster taken from the death mask of an adult female chimpanzee, adult and infant chimpanzee replicas, an adult human head replica, a juvenile chimpanzee skull with a movable jaw, the mounted skin of a spider monkey with movable head and shoulders, the curated hide of a juvenile chimpanzee and the corpse of an infant chimpanzee.

Some of the objects elicited intense fear or panic (in decreasing order: movable chimpanzee skull, snake cast, movable spider monkey skin, chimpanzee death mask), which Hebb interpreted as fears due to conflict; he suggested that the sight of mutilated bodies aroused an incompatibility at both the perceptual and at the cognitive level (Hebb, 1946). Butler (1964) tested rhesus macaques in a test-box where they could see through an opening into another box. This other box contained live snakes, a live conspecific, an anaesthetized conspecific or a dead conspecific with its head on its outstretched hands. Butler predicted that the more frightful the stimulus, the more suppressed the viewing behaviour would be. However, this was not the case, and Butler explained the monkeys’ reactions as a possible result of a psychological barrier between the subjects and the objects because no physical contact was possible. The decapitated monkey did elicit more looks than the live one, even though mean looking times were higher for the latter. This result might reflect a configural incongruity in the corpse eliciting a greater number of viewings but decreased overall looking time due to aversion (sensu the uncanny valley phenomenon).

How do these considerations help us advance our understanding of death awareness in non-humans in their natural environment? Boesch (2012) has suggested that wild chimpanzees have a capacity for the ‘causation’ subcomponent of a full-blown awareness of death. Chimpanzees of the Tai Forest (Ivory Coast) face higher predation risks than many other chimpanzee communities (Boesch & Boesch-Achermann, 2000); they exhibit more fearful responses to individuals that died of disease (10 cases) than those that show wounds due to leopard predation (5 cases). Furthermore, Taı chimpanzees lick the wounds of injured group members, but not the dead. If the reason for these differences lies in an understanding of reliable cues for death (grievous wounds, severe disruptions of the body envelope), then chimpanzees may have an implicit awareness of death, not only distinguishing between dead and alive, but also between different manners of death, potentially providing evidence for the subcomponent of causation.

## 4. Concluding remarks

With this review I’ve attempted to bring together observations of living individuals’ responses to dead conspecifics in vertebrates, evidence regarding the sensory bases of detecting life and death in others, and potential cognitive underpinnings for animals’ awareness of death. I suggest that phylogenetically ancient responses relating to death that are present in many animals exist not only for specific predator detection but also form part of a generalized threat detection mechanism. Presumably in corvids, cetaceans, proboscids and non-human primates, these mechanisms run in parallel with living–dead discrimination processes based on associative concept learning.

As further chapters will deal solely with non-human primates, to what extent primates’ (or indeed any taxon’s) responses to the dead are shaped by learning is an intriguing question. Witnessing death events can allow information-gathering about various sets of cues associated with the phenomenon that can be retrieved on similar subsequent encounters; active information seeking in such situations has been suggested, for example, in chimpanzees (Cronin et al., 2011). With respect to the extended carrying of dead infants, the eventual abandonment of the corpse by a mother may reflect her acquisition of some component of death-awareness, through a combination of visual, olfactory, and behavioral cues—or their lack of correspondence with those emitted by live infants. Social learning may also shape some thanatological responses: it has been suggested that witnessing dead-infant carrying by others may promote the behavior in mothers experiencing their own infant's death (Biro, 2011).

Experimental studies of thanatological responses in wild primates are largely lacking in comparison with corvids. Allen and Hauser (1991) proposed an experiment using playback calls (as done with vervet monkeys (*Chlorocebus aethiops*) with recently dead infants, to study concept attribution (e.g. cognizance of death) in non-human primates. Females, they argued, when presented with the playback would (i) orient towards the speaker and act as if the infant were alive, (ii) respond in a distressed manner and search for the infant, or (iii) not react at all and continue engaging in ongoing activities. To our knowledge, this experiment has never been implemented, possibly due to ethical concerns. However, a variation was conducted in a study of the strength of male-female relationships in free-ranging chacma baboons (Papio ursinus) (Palombit et al., 1997). The authors found that males responded to a female's call if there had been a close association (friendship) between them, but not if the female's infant had recently died. Their interpretation was that females, primarily responsible for maintaining these close associations, ended friendships with males upon their infant's death, either because they no longer needed a male to protect their infants or because they themselves no longer benefited from protection by the male. However, an alternative interpretation is that the males themselves chose not to respond on the basis of knowing that the infant had died (including, perhaps, knowledge of the event's irreversibility). I further suggest that inductive/analogical reasoning is (or could be) *a sine qua non* condition for human-like death awareness with all of its main subcomponents (*universality, irreversibility, cessation, and causation*), in non-human animals. As research on human children's acquisition of the concept of death suggests they use these higher-order reasoning skills to understand these subcomponents (Carey, 1985; Slaughter, 2005). Whether this claim will be further supported or necessitate a substantial revision will depend on the quality of the data in studies yet to come.

# Chapter 4. Evolutionary Foundations of Grief

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"*Observe how passionate and yet how brief is the sorrow of dumb animals. The lowing of cows is heard, for one or two days only, and that wild and frantic running about of mares lasts no longer; wild beasts, after following the tracks of their stolen cubs, after wandering through the forests and returning over and over to their plundered lairs, within a short space of time quench their rage; birds, making a great outcry, rage about their empty nests, yet in an instant become quiet and resume their ordinary flight; no animal has a prolonged sorrow for its offspring except for Man, who clings to his grief and the measure of his affliction is not what he feels, but rather what he wills to feel.*"

(Lucius Seneca, 40 AD, *On Consolation to Marcia*, Dialogue 6)

"*If it chaunce that their master bee oppressed, (…) by the greater violence, and so be beaten downe that he lye groveling on the grounde, (it is proved true by experience) that this Dogge forsaketh not his master, no, not when he is starcke deade; but induring the force of famishment and the outrageous tempestes of the weather, most vigilantly watcheth, and carefully keepeth the deade carkasse many dayes, endevouring, furthermore, to kil the murtherer of his master, if he may get any advantage*"

(John Caius, 1576, *Of Englishe Dogges*, pp. 30)

"*Every perturbation is a misery, but grief is a cruel torment, a domineering passion (…), when grief appears, all other passions vanish. It dries up the bones, saith Solomon, makes them hollow-ey'd, pale and lean, furrow faced, to have dead looks, wrinkled brows, shriveled cheeks, dry bodies' and quite perverts their temperature that are mis-affected with it*"

(Robert Burton, 1651, *The Anatomy of Melancholy*, pp. 225-226)

## 1. Defining Grief, Bereavement and Mourning

In his book *The Expression of the Emotions in Man and Animals,* Charles Darwin argued for an evolutionary continuum in emotions between humans and other animals. In a chapter discussing grief, he identified two states; *excessive grief* and *sorrow*. The former was described as "frantic" and "energetic" whereas the latter was "languid" and "dull" (Darwin, 1872). Since our primate relatives do not weep or show the facial expressions associated with sadness or depression, Darwin concluded grief to be a typical human response. But even Darwin was not definite in this conclusion making other claims suggesting either the contrary or taking an agnostic position (Darwin, 1871; 1872). But, as we will see later on, this dual character of grief Darwin formulated, one more active and another more passive, is seen again described during the 1960's research on mother-infant separation among non-human primates (Gilmer & McKinney, 2003) and later evolutionary accounts for grief (Archer, 1999).

Currently, what is meant when we invoke terms such as *grief*, *mourning*, or *bereavement*? Often, in the human literature, these concepts are vague or confused with each other, however, by looking at where they converge the most, we can achieve clearer definitions. *Bereavement* can be defined as the status/period of an individual facing a loss due to the death of a loved one having a temporal aspect during which *grief* is experienced and *mourning* is manifested. It is a dynamic, universal, and but also individualized process with a normative component. *Grief* is characterized as the emotional, physiological, cognitive, or behavioral responses towards the loss of a conspecific, pet, or even an object. This response is triggered by physical separation (perceived loss) or the result of death (actual loss). *Mourning* is a process manifested through outward behavioral manifestations of grief which are themselves (in the case of humans) ritualized in character and tied to social/cultural factors such as death rituals/practices that ultimately have a coping purpose. Thus, where a clearer distinction can be found between *mourning* and the other two terms, *grief* and *bereavement*, what also transpires is that *grief* is better understood not as a basic emotion but as a prolonged state in which a constellation of emotions can arise (i.e. sadness, anger, guilt, etc).

## 2. Evolutionary Accounts of Grief

Taking a more comparative approach with an evolutionary basis, Archer (1999) defines grief as an emotional response triggered by loss and characterized by *active distress* and *passive depression*, which is universal in human cultures but also observed in social mammals and some birds following the loss of a parent, mate or offspring. As encompassing as Archer's definition is, one can make a prediction this will not extend to only social mammals as there is a mother-infant bond character in grief. Additionally, because there is a pair-bond component in grief, it is not unreasonable that we will see analogous responses in pair-bonded taxa to loss that are not necessarily avian or mammalian, such as fishes (Laubu et al., 2019) or reptiles (Kerr & Bull, 2001), but whether these are actual displays of grief and not extensions of *mate-guarding* remains to be seen.

The main reason for these bonds resides in phylogenetically ancient caregiving mechanisms that are mediated by neuropeptide hormones such as *oxytocin* (in the case of mammals), and its homologues, such as *mesotocin* (in the case of birds, reptiles, and fishes). Among vertebrates, such hormones originally served a purpose for "basic" reproductive behavior (vocalizations, courtship behaviors, nest building) and then were extended towards more "advanced" reproductive behavior (pair bonding and parental care) which then culminated in the formation of social bonds and their maintenance (reviewed in Knobloch & Grinevich, 2014). While there are many explanatory hypotheses on the evolution of grief, a thorough reading of the literature makes it clear that it is first and foremost caused by the severance of bonds. Thus, the loss of a parent, mate or social partner can be detrimental to an individual's fitness and will trigger an emotional imbalance whereupon the individual will either engage in calls or initiate a search for the missing object of attachment in an attempt to reach homeostasis.

## 3. Conspecific Separation & Grief Studies

Seminal research on mother-infant separation was mainly done in non-human primates (Jensen & Tolman, 1962; Seay et al., 1962; Hinde et al., 1966; Kaufman & Rosenblum, 1967) but also, to a lesser extent, rodents and canids, to study comparative models of depression have highlighted the emotional and behavioral responses to separation in infants. This research described, or rather, rediscovered after Darwin, two states; *protest* (categorized by marked increases in movement and vocalizations) and *despair* (substantial reduction in activity and intensification of self-directed behaviors). Rather than stages (as these do not follow each other in a sequential manner and alternate between themselves), these states were accompanied by changes in body temperature, heart rate, endocrinal/immune system, and neurochemistry, together with decreases in food/water intake, perturbations of sleep, and in some cases these experiments were followed by death (Spencer-Booth & Hinde, 1971; Reite et al., 1978; Gilmer & McKinney, 2003).

This research had, in fact, its main inspiration in the human medical reports. During the 1940's research done on maternal separation on infants, mainly by Harry Bakwin, William Goldfarb, and René Spitz, highlighted the adverse effects early separation and hospitalization had on those infants. Their work on depression influenced greatly Harry Harlow who then started the blueprint for the mother-infant separation studies in rhesus macaques and John Bowlby who formulated the *attachment theory* that these and subsequent studies are now grounded on (van der Horst & van der Veer, 2008). The states aforementioned in non-human animals were borrowed from Bowlby’s three-phase formulation in human children´s response to separation: *protest*, *despair,* and *detachment*. Children in these states exhibit behaviors that bear an uncanny resemblance to non-human primates. In the *protest phase,* they engage in crying and moving about, having tantrums, and searching for the mother, whereas in the *despair/detachment phases*, they become apathetic and withdrawn, sometimes breaking into “a monotonous wail” (Bowlby, 1960).

Highlighting yet again the close similarity between humans and other mammalian species, in reviewing decades of research on common grief in humans, Bonanno and Kaltman (2001) describe distinct types of disrupted functioning in bereaved individuals. These were as follows; *cognitive disorganization* (confusion and preoccupation), *dysphoria* (distressing emotions, yearning, and loneliness), *social withdrawal* and *isolation* (role disruptions and difficulties forming new relationships), *health deficits* (loss of appetite, restlessness, and insomnia) and *neuroendocrine/immune functioning* (cortisol elevations[8] and reduced lymphocyte responsivity).

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[8] Originally contested in Bonanno and Kaltman (2001), further evidence for cortisol increases during bereavement is shown in Hopf et al. (2020).

# 4. Ethological observations in non-human animals

Figure 4.1. Adam and Eve with their keeper at the Philadelphia Zoological Zoo Gardens *circa* 1876. This image is in the public domain.

As with the comparative conspecific separation studies, naturalistic observations both in captivity and in the wild, especially in non-human primates, illustrate the eerie similarities they show with bereaved humans. In what is now regarded as the first paper on comparative thanatology "*Grief in the chimpanzee*", Arthur Brown (1879), described two juvenile chimpanzees (Adam and Eve) that lived together in the Philadelphia Zoological Gardens and the behaviors of the male shortly after the female died. Upon her death, the male attempted to rouse her body by lifting her head and arms and further moving the body around. At first, the author describes the male as yelling of rage which was then followed by plaintive sounds. When the keepers attempted to remove her body, Adam was at first violently opposed to this, after her removal he only calmed down if the keeper was together in the enclosure with him, however, when accidentally catching a glimpse of the body through the doors he became agitated again. On the following days, Brown describes Adam's behavior as listless and at times producing moans. In her absence, Adam became more attached to the keeper and became reluctant at him leaving the enclosure. Before Eve's death, both chimpanzees slept with a blanket on the floor, after her demise, Adam started sleeping on the top of the enclosure (see Figure 4.1). There are several such accounts in the literature, most relating to non-human primates with few exceptions since the evidence for grief in other taxa within these contexts is mainly limited to grey literature.

### a) Bereaved Infants

During her field research in Gombe Tanzania, Jane Goodall (1986a) witnessed the behavioral and physical changes of nine orphaned chimpanzees, which included lethargy, decreased play, loss of appetite, and emaciation. She recounts the cases such as the juvenile Pax that became agitated and screamed when his mother Passion died. He pulled her hand constantly and stayed in proximity with her body along with his two elder siblings for hours, then moved away before nightfall. The case of the juvenile Flint was the most severe. Flint who was considerably attached to his mother Flo, according to Goodall (1990), fell into a depressive state after her death, becoming withdrawn, refusing to eat any food that was offered, and three weeks later he passed away. The common explanation given is that Flint died likely due to an immunosuppressed state that made him susceptible to illness. The autopsy showed there was an inflammation to his stomach and abdomen. Frans de Waal (1996) pointed out as an alternative that Flint simply caught the same illness that Flo had and endured it for three weeks longer. However, considering there are reports of macaques (Spencer-Booth & Hinde, 1971) and langurs (Dolhinow, 1980) dying after separations in captivity with no apparent illness, and given that there was no body in sight (Flo was buried by the field researchers), both explanations for Flint’s demise are not necessarily mutually exclusive. Also in Gombe, Botero et al., (2013) report that two wild adolescent chimpanzees, 1-2 years after the death of their mothers, exhibited overall low rates of social exchange, less playful behaviors, and higher rough self-scratching when compared to other peers in the same community. Both Goodall (1986a) and Botero et al. (2013) reported *rocking behaviors* in orphaned chimpanzees just as, decades before, Spitz and Harlow observed these in their human and macaque subjects respectively.

Some reports of wild monkeys are also available. In gelada baboons, such rocking[9] has also been described when an orphan 7-month-old (Tussock) was seen vocalizing beside her mother who succumbed to an infection. Having both been separated from the group, Tussock died on the next day (Fashing et al., 2011). This is usually the fate of orphans still dependent on their mothers in the wild, unless adoption by another female occurs (Thierry & Anderson, 1986), although not all adoptions are successful. Perry and Manson (2008) describe the case of an 8-month-old capuchin infant male (Cebus capucinus) whose mother was killed by poachers; the infant spent the whole day next to her body "cooing and trilling piteously" and attempting to nurse from her body.

Mohnot (1980) gives us the most detailed account of infant grief-like patterns to date. In it, he describes a 28-week-old hanuman langur's response to the death of her mother over the course of 58 days after which she disappeared from the group. When her mother fell from a tree after being struck with a rock, apparently dying shortly afterward, the infant came down the tree and initiated physical contact with the deceased mother giving out vocalizations (pulling the hair on the back, touching the face, tail, and back, forcing her face into her chest and screaming loudly and cooing). During the first hour, she began a back and forth pattern of going up a tree branch and returning to the corpse. Other group members went down the tree and approached the corpse as well. In succession, three females held the infant preventing her from approaching the corpse which caused the infant to scream louder. Besides four females trying to hold the infant, she also rejected embraces from other juveniles and infants in the group. In the second hour, group members would occasionally descend from the tree and check on the corpse then return. In the third hour the infant

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[9] It is unclear to the authors of this study, however, if Tussock was engaging in this rocking behavior as a lack of contact stimulation or as a result of the cold (King, 2013).

descended the tree to her dead mother and was joined by an old female and her infant, all three returning. When the body was removed the next day, the infant screamed, and together with the old female followed the cleaners for about 50 meters. In the following days, the old female adopted the orphan. Her behaviors were consistent with the mother-infant separation literature, she showed little interest in playing or eating, engaged in thumb-sucking, and self-clutching, apathetic towards social interactions with exception of her foster mother. From the 38th day onwards, Mohnot notes the infant began showing indifference towards her foster mother, while her feeding increased, her vocalizations decreased, and submissiveness increased. Finally, 20 days later, she disappeared from the group, the author postulating she either died and was eaten or was captured alive by predators due to her inactive demeanor.

Murray and Rutherford's empirical study report that the death of a captive adult female Asian elephant (Sithami) affected her 18-month-old calf (Aayu) the most in comparison to the group; he spent more time alone, his playful behaviors decreased, which at his young age could not be attributed to maturation but more parsimoniously due to maternal deprivation (Murray and Rutherford, 2021).

For African elephants, Bradshaw (2009) collected a few cases from a Kenyan Sanctuary. Two 3-month-old calves, Mailaka and Ndume, from the same group were separated from their families after being attacked by farmers, were described as listless and suffering from disturbed sleep[10] afterward. Malaika, who was recovering from slashing wounds to her leg initially euphoric at being cared for by the keepers, fell into a "depression that lasted for weeks", whereas the effects for Ndume were more pitiful. Having regained consciousness from a headwound, Ndume started to "cry pitifully" and producing a shrill trumpeting, presumably, for his mother. Both elephants

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[10] Anderson et al. (2010) also refer to sleep disturbances following death in their captive chimpanzee population.

showed signs of distress and would, according to Bradshaw, suffer from nightmares waking up at night and bellowing. Ndume's distress was more pronounced as he had to be let out of the sleeping stable, initiating a frantic search, it was believed, for his mother. Other comparable cases[11], such as Mzima and Dika are recounted. Mzima, a young bull who had been lost from his family, was struggling by himself in the wild even going as far as following a zebra herd. When brought back, he seemed contented even playing with other orphan elephants, but sank into a depressive state after a week becoming socially withdrawn. On the other hand, attempts at comforting Dika, who had observed his mother's slaughter, were unsuccessful for weeks, Dika at one point almost died (Bradshaw, 2009).

The long-term effects of these traumatic events (culling and poaching) are hypothesized to be the root cause of what Bradshaw et al. (2005) term *elephant social breakdown*. This definition they use to describe abnormal sets of behaviors some orphaned elephants go on to exhibit such as an inability to cope with stress-reactive situations resulting in increased aggression. This is particularly the case in younger males who without the socialization with older experienced males, will experience earlier *musths* (period of heightened hormonal and sexual activity), whereas introduction of older males to these groups halts such maladaptive behaviors.

### b) Bereaved Progenitors and Peers

Often, the death of an offspring will too trigger an observable grief-like response in the progenitors, usually the mother. Following its death, reports confirm social readjustments, in the form of the bereaved individuals strengthening their social bonds with other individuals in the

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[11] Morell (2013) gives us an interspecies insight: recounting the case of an orphan elephant that "shrieked and moaned" when it discovered the buried remains of a poached rhinoceros it was closely bonded with.

group. Returning to the wild chimpanzees of Gombe, Goodall (1990) recounts the case of Pom, who became lethargic and even emaciated to a life-threatening point, after her infant died from a fall, ultimately, she readjusted by developing a closer relationship with her mother Passion. Illustrating this newfound social reliance, Goodall reports on one occasion, having become separated from Passion, Pom whimpered frequently for an hour while looking for her mother until the reunion. De Waal (1996) gives a vivid account of a captive chimpanzee female in the Arnhem Zoo that would whimper and wail following the loss of her infant (see also Blair, 1920).

There are other consequences from the loss of a conspecific that indicate coping or social readjustment. In mountain gorillas, Fossey (1983), albeit not describing any overt signs of grief, reported primiparous females (whose infants were lost to infanticide) engaging and playing more with a juvenile as a way, the author suggests, to strengthen social ties. Orgeldinger (1996), describes significant behavioral shifts in captive siamangs (*Symphalangus syndactylus*), in the breeding couple following the death of their infant, notably, increased levels of play, bonding, and sexual and agonistic behaviors with decreased levels of territorial behaviors.

Anne Engh (*in* King, 2013) relates to us the story of a chacma baboon mother-daughter pair (Sierra and Sylvia, respectively) who were high-ranking and remarkably close-bonded. When Sierra was predated by a lion, Engh noticed some behavioral changes in Sylvia; for a week or two she wouldn't initiate social interactions and sat at a distance from other troop members, appearing "depressed". This prompted Engh to initiate an endocrinal study on baboon bereavement. Engh and colleagues (2006), recorded a total of 26 deaths, most due to predation. They found that stress levels (measured by fecal glucocorticoids) increased after four weeks when compared to control females.  Following these events, the "bereaved" females appeared to be coping by widening and reinforcing their grooming networks, thus helping return their stress to baseline levels.

Supplementary findings by Seyfarth & Cheney, 2013) point to temperamental differences impacting the success of these bond reformations after the death of a relative (i.e., more social individuals coped better than aloof individuals). Kaplan et al (2012) also report similar findings in common marmosets; while not the primary concern of their research, they managed to record more than double the stress levels in the group, following an accidental death of a roommate, and these remained high for 3 days. A recent publication (Takeshita et al., 2020) found again increased cortisol levels in one Japanese macaque female that lost her infant.

Social withdrawal in non-human primates seems to be a common behavioral expression during bereavement. According to observations in wild Japanese macaques, after their infants died, the mothers would exhibit low activity levels and a sagging posture, and an overall "depressive" appearance paired with social withdrawal[12] (Green, 1975). Similar withdrawal has been reported in wild snub-nosed monkeys, describing the females retreating from social activities during the first days following their infant's deaths (Li et al., 2012; Guo et al., 2016). The loss of an established group member can result in behavioral shifts in the group such as appetite reduction and decreased activity levels. This has been reported in captive populations of chimpanzees (de Waal, 1996;2013; Anderson et al., 2010) gorillas (Less et al., 2010) and orangutans (Herzfeld, 2016). Moreover, several accounts in chimpanzees have described silence in the group following a death, either by fatal aggression (de Waal, 1986; Pruetz et al., 2017), disease (de Waal, 1996, 2013), or old age (Anderson et al., 2010).

Second to non-human primates, our best data comes again from elephants. As with other species, observations on elephant grief-like responses, historically, have been confined to

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[12] In some of these cases, it remains problematic to ascertain whether social withdrawal is an active choice by the mother or the results of others moving away from her dead infant, presumably because of the smell (Gonçalves & Carvalho, 2019).

anecdotes like Joyce Poole's observation of an African female elephant standing by her stillborn calf for three days with tears running down[13] and with a demeanor that "spelled grief" (Poole, 1996, p.95). Additionally, more recent empirical studies have been published. In two captive Asian elephant groups (Oregon Zoo and Smithsonian National Zoological Park), Glaeser et al. (2020) reported six deaths (4 adult females, 1 adult male, and 1 female calf) experienced by seven adult female herdmates. Measuring the cortisol concentrations (urinary and serum) over a period of up to 45 days, they found living herdmates' responses varied. Following the death of the calf (nzF1) no significant increases in cortisol were found in the group. The deaths of two females (ozF2 and F6NZ) did not produce a significant increase in cortisol in the herdmates. The death of the adult male (ozM1) produced a significant increase in cortisol in one of the two females whereas the death of a female (F4OZ) produced a significant increase in cortisol in two of the three herdmates. Likewise, following the demise of (ozF1) produced a significant decrease in cortisol in one of the two herdmates. As the authors suggest, these varying findings (low rate of change in glucocorticoid activity) represent only one measure of response to social change, other measurements are possibly needed to complement the results. This differential nature of Asian elephant's responses towards death is again illustrated in another anecdote where three female elephants (Tarra, Winkie, and Sissy) at a Sanctuary refused to eat or drink following the passing of another female (Tina), two of which stood over her body the first night. Whereas Sissy remained silent, Winkie was distraught and nudged Tina's body. After her burial, Tarra vocalized, Winkie paced around, and Sissy remained silent. The following day Sissy left her tire (which she carried often) over Tina's grave for several days (King, 2013). Rutherford and Murray's study offer a more empirical approach by measuring behavioral and temperamental changes following a death in a group of captive Asian

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[13] Elephants are known to secrete fluids from their temporal glands (close to the eye regions) during periods of intense emotional arousal.

elephants from Chester Zoo. When compared to baseline levels the death of two calves produced an increase in affiliative and social behaviors in herdmates the inverse trend was observed, overall, when an adult female died. The authors suggest the death of an established group member such as a female adult affects the entire herd rather than a calf which mainly affects the mother, although diverse relationship qualities will have varied behavioral responses to death depending on the individual (Rutherford & Murray, 2021). While it stands to reason these behaviors are more widespread than previously believed, it remains difficult to observe certain animals either because they are elusive, or like cetaceans, they live in aquatic environments that make direct observations challenging. Morton (2002) gives us an account of  Corky, a captive orca following the loss of her calf. She emitted distress or lost calls and refused to eat for 3 days, while a more widely known case is that of the wild orca J35 (Tahlequah) that carried her calf for 17 days covering about 1600 km (Shedd et al., 2021). In wild cases such as J35's, it is also difficult to disentangle whether the decreases in appetite are directly related to efforts to keep the calf afloat and other caretaking responses, rather than as a result of grief *per se*, although Corky's anecdote and others do suggest a grief-related response.

Concluding, we have examples of rabbits from a rescue organization (HRS) that allows the animals to interact with their peers after they are euthanized. Davis & DeMello (2003) dedicate a chapter of their book to this topic relaying to us stories such as Benjamin who stopped eating after his peer died of kidney failure, himself dying shortly after, or Jake who became aggressive with other group members after his mate died, or Elmo who was active and playful, following the passing of his mate, became "subdued" and "depressed". These are, of course, some of the many ways Davis & DeMello (2003) report on rabbits' behavior following death (see also Smith, 2005). The most parsimonious explanation is that such variation depends on personality and bonding the individuals have with each other, although it should not be discounted the possibility of unrelated cause-effect interpretations in some cases. Many such anecdotes are recounted in popular science books ranging from wild animals to farm animals and domestic pets (Masson & McCarthy, 1995; King, 2013; Safina, 2015).

## 5. Grief, Empathy, and Conceptualizing Death

"*Monkeys almost never comfort each other after the loss of a close relative, look after sick group members, provide food for the old or disabled, or manifest any other forms of care that we like to think of as natural components of human interactions. (...) One possible explanation is that compassion demands some understanding of another's needs and purposes, an ability that monkeys may not possess if they cannot attribute states of mind to others. Unlike monkeys, chimpanzees do sometimes appear to show compassion. (...) But do chimpanzees ever show empathy? Goodall describes a number of instances in which chimpanzees apparently experienced mental depression, grief, and a sense of loss when a close relative died. What is striking, however, is that in none of these descriptions is another animal ever reported to have consoled a grieving companion.*"

(Dorothy Cheney & Robert Seyfarth, 1990, *How Monkeys See the World*, pp. 236-237)

"*Equally striking, however, is the absence of sympathy among other chimpanzees: no chimpanzee has ever been reported to have consoled a grieving companion. Although chimpanzees have mental states and grieve at the loss of close friends, they do not seem to recognise the same mental states in others. As a result, they are unable to share another's sorrow or show empathy towards it.*"

*(Robert Seyfarth & Dorothy Cheney, 1996, Inside The Mind of a Monkey, p. 342)*

Cheney and Seyfarth (1990;2007), have many times pondered the possibility of a qualitative difference among great apes versus monkeys regarding mental state attribution. Still, they argued, that in the absence of more systematic observations, current anecdotes intriguing as they might be, do not settle the question but only provide us with "hints" or possibilities of an investigation into these topics. They also seem to be operating on a strictly cognitive explanation for empathy, which albeit not a completely incorrect assumption, does not account however for simpler/automatic aspects inherent to empathy. This is also reflected by their interchangeable use of the terms *compassion* and *empathy*. *Empathy* can be explained as *feeling for* as in sharing a feeling of suffering or distress for the other, whereas *compassion* can be understood as *feeling with* as in sharing a feeling of concern and care with a motivation to act for the wellbeing of the other (Singer & Klimecki, 2014).

But before we return to this issue, let us consider first the form and function of these so-called *consolation behaviors* in the primate order and identify to which extent these fall on the *empathy-compassion* spectrum. Hilary Box (1984) reports the death of a captive female common marmoset during which the male spent some time grooming her and scent marking. After she was removed, to which the male protested, their eldest daughter groomed him attentively while also scent marking. The whole group became calm within minutes of the removal of the corpse. Box suggested that, without the mother, the eldest daughter appeared to be assuming her role. Another account, involving a young Japanese macaque, describes her clutching her dead infant and wailing, following this she was embraced by her mother (Green in Pierotti & Annett, 2014). Similar embraces are described previously in langurs (Mohnot, 1980) as the three adult females that intercepted and embraced the agitated orphan preventing her from approaching her dead mother.

These events illustrate the difficulty in interpreting and attributing to them functional terms such as *consolation*. But two papers involving captive chimpanzees give us a better picture. Yoshida (1994) describes in a short report the accidental death by hanging of a juvenile chimpanzee (Jacky). The following day, the author reports the mother (Jarny) vocalizing, seemingly, at the rope that killed her son, the other group members stayed in close proximity for longer durations than usual and groomed her. Additional support for the idea that chimpanzees might in fact console bereaved group members was recently found by Goldsborough et al. (2020). In a Sanctuary, they found that, when a chimpanzee mother lost her infant, the group members displayed high levels of reassurance behaviors that same day, furthermore, they increased affiliative responses days following her loss. These interactions were measured against a control female that had not lost her (both females were recent arrivals). While these do not completely settle the question of whether primates (and other non-human animals) show compassion towards a bereaved conspecific, they do show some support for such a proposition.

The question seems yet partially unresolved since even if we do find consolation behaviors are not as rare and are indeed expressed in some fashion among non-human animals, from the available evidence alone it is not clear what the underlying motivation of the consoler is towards the bereaved group member: are they solely empathic or are they compassionate? Do they arise from an understanding that the bereaved members are in emotional suffering due to their loss or, more simply responding to their emotional state by engaging in consolation behaviors in an attempt to decrease the distress in the bereaved regardless of any causal attribution to their condition? The most parsimonious explanation in some of these examples (if not all) seems to be the empathic rather than the compassionate explanation. Empathy is interpreted as being at the root of sympathy or compassion, it does not operate solely on cognitive levels, at its basis being a spontaneous emotional contagion response (de Waal, 2008; de Waal & Preston, 2017). And, while many animals have been seen displaying compassionate behaviors towards sick, dying, and dead individuals (Fashing & Nguyen, 2012, Gonçalves & Carvalho, 2019), very rarely have they been observed comforting bereaved individuals. In Barbara King's book in which she extensively reviewed grief responses in several animal species, no such *consolation behaviors* directed at grieving individuals are to be found (King, 2013). There are two ways of considering the paucity of data in this regard, either they are missed in these observations or, the animals simply lack the necessary cognitive adaptations to do so (*sensu* Cheney & Seyfarth, 1990), being only limited to recognize and provide them to sick/dying individuals. *Contra* Cheney and Seyfarth's *no-consolation predicament*, the existing data from chimpanzees suggest these abilities might have been understated, but more research is needed.

Moreover, these grief-like responses do not necessarily presuppose a full awareness of death (King, 2013). As I have argued, there are experimental and observational reports that make a strong case for shared critical features and an overall evolutionary continuum between humans and non-human animals (mainly vertebrates) regarding grief. From both the experimental and ethological evidence we find these features are shared at 1) the etiological level, 2) the behavioral level and 3) the neurophysiological level. These manifest following death/separation of kin, mate, or peers. From an evolutionary perspective, physical disappearances mimic a loss through death, thus to the bereaved, both corpses and disappearances activate the same distress-depressive states. Since very young human children, arguably, like non-human animals lack a concept of death (or at least a developed one), these reactions towards separation are equivalent to those towards dead bodies (Archer, 1999).

Based on his experimental work, Jaak Panksepp proposed the existence of seven primary process emotional systems in the neural pathways of the mammalian brain, and of particular importance the Panic/Grief and the Seeking/Desire systems (Panksepp, 2004; Panksepp & Watt, 2011). The Panic/Grief System is a critical opioid modulated system that helps to promote social connections (mother-infant bond and social attachments). It endures hyperactivity (reflected by loss of social bonds and psychological pain), which on a first level is characterized by a distress phase and then followed by a despair phase characterized by low arousal in the Seeking/Desire System (reflected by amotivational states and dysphoria). These primary process emotional systems are located in evolutionarily ancient subcortical brain regions and shared by all mammals and with homologous regions in birds (Panksep & Watt, 2011; Panksepp, 2017). In light of this, while human grief may be mediated by language and culture, it still lies in an evolutionary continuum originating in anatomical structures and chemical processes in the midbrain and lower brain structures, which are phylogenetically old. To put it in Randolph Nesse's words *"We humans know that death is permanent, but we nonetheless persist in reactions that are fundamentally similar to this searching behavior in other animals"* (Nesse, 2005, p.203-204).

# Chapter 5. Comparative thanatology of non-human primates

## 1. Introducing the primates

Non-human primates share a close evolutionary trajectory with humans, as such, they remain the best candidates to investigate how our ancestors before the Homo lineage might have responded to death, preceding the emergence of ritualized behaviors towards the dead – arguably one of the defining traits of our species. Where recognizing a corpse is evolutionarily advantageous for a species, natural selection will act on it. Several species in the animal kingdom (comprising eusocial insects, fishes, and rodents) exhibit either/both necrophoric or necrophobic behaviors 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 behaviors, 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 – behavioral trends they share with corvids, proboscids, and cetaceans (Gonçalves & Biro, 2018). Although the number of publications has been increasing 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 synthesize the available primate thanatological data (Box, 1984; Vieira, 1987; Anderson, 2011).

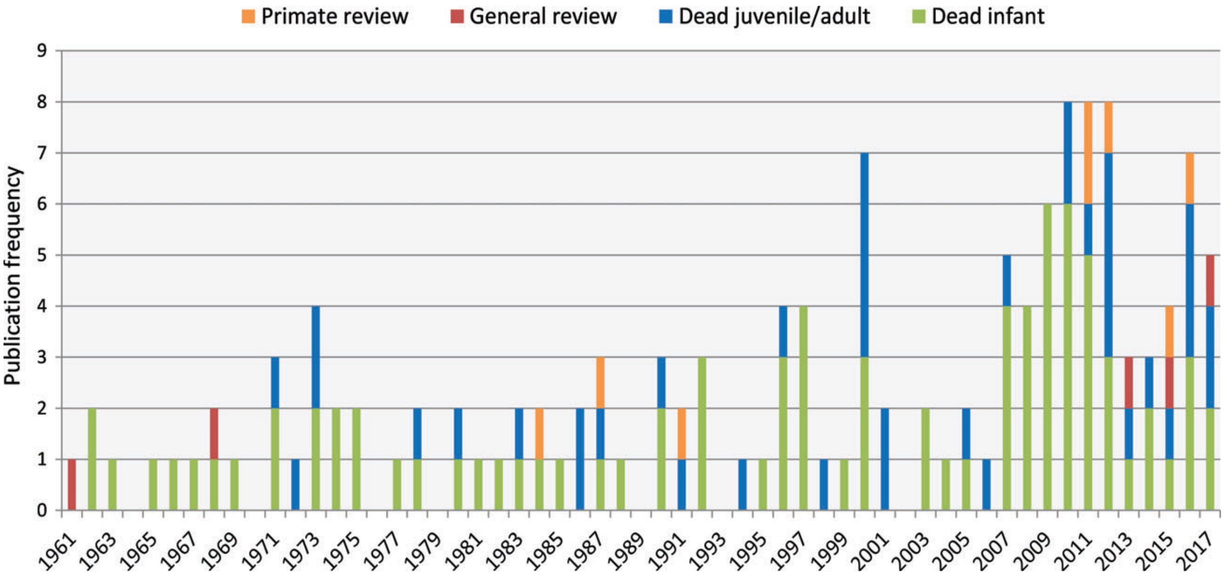

Figure 5.1. Publication frequency on the subject of primate thanatology from 1961 to 2017. The search was conducted in www.scholar.google.com using the key words: "dead"/"deceased" + "infant"/"conspecific" and the corresponding genus (i.e. Macaca, Pan).

### 1.1. 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).

Eugene 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).

### 1.2. 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, 1986a). 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, 1986a).

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

### 1.3. Experimental/quasi-experimental research

Primate thanatology has not been outside the experimental sphere. Besides key studies exploring grief-like responses using the infant-mother separation paradigm (Jensen & Tolman, 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, (see Chapter 1 p15) Gordon Gallup, whose insightful experiments with mirror self-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).

### 1.4. 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; Guo et al., 2016; Yang, Anderson & Li, 2016) and Indian (Balasubramanian & Sabu-Jahas, 1997; Rajpurohit, 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; Cronin et al., 2011; Fashing 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).

# 2. Contemporary Reports

## 2.1 Reports on 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 (see Figure 5.2). 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 (see Table 1.1), 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).

Figure 5.2. 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).

Table 1.1. Dead-infant carrying hypotheses

| | |
|---|---|
| Unawareness hypothesis | The mother may be unaware or unsure 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, $\beta$-endorphin peptidergic, and noradrenergic systems that promote and reinforce maternal behaviour, expressed in higher sensitivity to sensory signals from the newborn (Kevern, 1988). These hormones, which are crucial to the 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 et al., 2008). |
| Infantile cues hypothesis | Dead infants retain infantile cues (size/proportion, colouration, facial features) that make them attractive for females to carry them (Jay, 1962; Alley, 1980). |
| Learning-to-mother hypothesis | Nulliparous females' interest and willingness to carry dead infants positively impacts their maternal skills (Warren & Williamson, 2004). |
| Parity hypothesis | More experienced mothers (i.e. multiparous females), presumably tend to carry dead infants for longer periods (Nishida, 2012; Sharma et al., 2011, but see Sugiyama et al., 2009). |

### 2.1.1. Mother–infant dynamics

Dead-infant carrying is the most prevalent thanatological behaviour distributed in several primate taxa. This should not be surprising since: (i) primates follow a typical trend observed in many vertebrate species of high infant mortality (Bronikowski et al., 2011); and (ii) 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 (Altmann, 1980; Shen & Su, 2008; Dellatore, Waitt & Foitova, 2009; Watson et al., 2015; Tian et al., 2016; Tokuyama et al., 2017; 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.

### 2.1.2. 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) (see Figure 5.3), 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.

Figure 5.3. A female crested macaque (Macaca nigra) hampers an attempt by another group member to inspect her dead infant. (credit: Andrew Walmsley).

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 emanating from the corpse. However, among chimpanzees (Biro et al., 2010) and Geladas (*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).

### 2.1.3. Old World–New World dichotomy

Currently, there exist only a few dozen published cases of dead-infant carrying among New World monkeys, comprising cebids, and atelids. The lack of information on this behavior may be partly due to the smaller number of publications on New World primates. Anderson (2011) argues that their tropical habitats may accelerate the decay of corpses and consequently their abandonment. Additionally, while Old World monkeys can be either predominantly 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 (Rajpurohit, 1997; Sugiyama et al., 2009; 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). A recent publication by Georgiev and colleagues (2019) illustrates the need for more records on arboreal species, depicting two cases in colobines (*Piliocolobus kirkii*) in which one infant was carried for only two days, but, surprisingly another was carried for an estimated two-weeks, seen in an already mummified state.

### 2.1.4. The non-carriers

Not all primates engage in corpse carrying although there is evidence that they do show behavioral responses to dead or dying infants. Strepsirrhines and callitrichines 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 behavior towards dead/dying infants. One individual carried her dying infant tripedally for 15 m, whilst others in the troop showed affectionate behaviors, 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, vocalize, 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 anesthetized 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 behavior 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). Recent detailed observations by Thompson et al. (2020) 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 hours with one adult male remaining in an apparent vigil after the rest of the group left. There seems to be a male bias in this species as well with regards to investment towards the dead infant, as there is generally more male involvement in infant rearing among callitrichids (Digby, 1995; Thompson et al. 2020; Brügger & Burkart, 2021).

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 may not engage in bipedal carriage) (see also Rumbaugh, 1965).

### 2.1.5. 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 (see Figure 5.4). 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

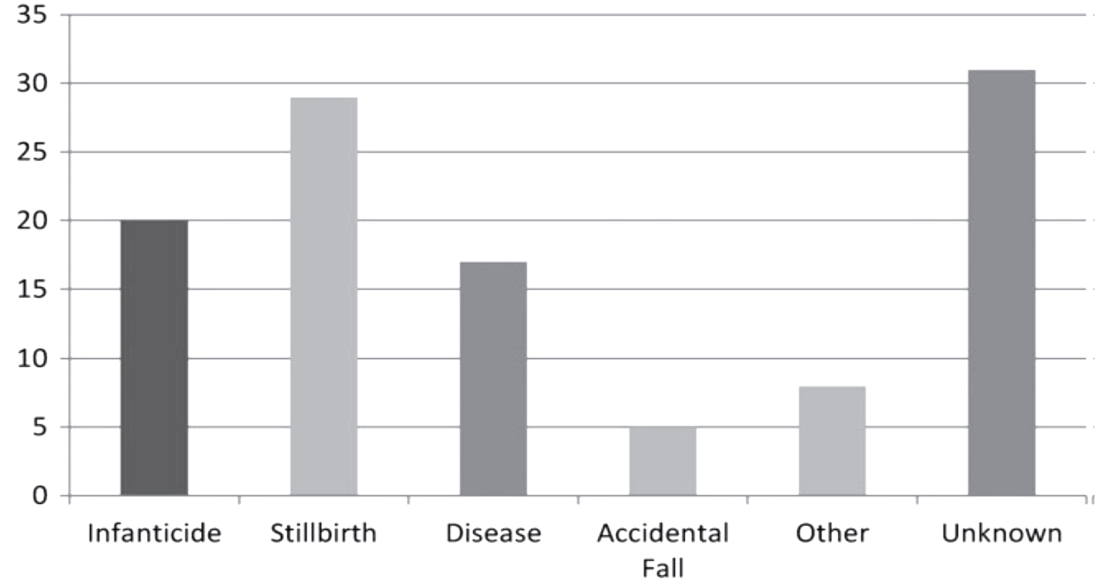

Figure 5.4. Cause of death in cases of dead-infant carrying collected from single case reports (N = 110) (Gonçalves & Carvalho, 2019).

cases of infanticide. 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 (i) 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 (ii) 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 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 behaviors 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. Defense and abandonment also occur with live infants.

Reviewing 59 cases of observed infanticides in New World and Old World primates, I found that about a third of the infants were carried by their mothers (N = 20), compared to two-thirds that were not (N = 39). 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.

## 2.2. Reports on dead group members (including juveniles/adults)

To some extent, interactions of living members towards dead/dying individuals indicate their prior relationship quality. There is a tendency that living group members to 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. 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; Campbell et al., 2016; van Leeuwen 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 organization 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 (Hofer, Huffman & Ziesler, 2000; Hosaka et al., 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 responses to death by adult conspecifics.

### 2.2.1. 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. 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; Biro, 2011; Cronin et al., 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 behaviors 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 monopolize the corpse and incorporate it into aggressive displays (Fossey, 1983; Buhl et al., 2012; Stewart 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 behaviors towards its dying mate such as alarm calling, embracing, sniffing, and protecting the corpse. Other behaviors 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 favorite 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.

### 2.2.2. Guarding the body

Guarding a corpse against perceived predators, typically expressed as mobbing behavior, 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 defense 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 against 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 guarding an infant's body while the mother forages, and individuals will band together to defend the corpse (Cheney & Seyfarth, 2007). Guarding responses share behavioral traits with sympathetic concern and empathetic targeted helping (P´erez-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).

### 2.2.3. Vigils

Vigils are characterized 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) (see Figure 5.5). 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, 1999). An adult male howler monkey (*Alouatta palliata*) was reported to stay in the vicinity of a female's corpse for 5 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 behavior. 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.

Figure 5.5. 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).

### 2.2.4. 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 behavior 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. 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 the 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 & Muhumuza, 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 the 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, personal communication), although this has not yet been reported 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; Matsumoto-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 odor 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 behavior (for fearful responses to abrupt deaths see Teleki, 1973; Boesch, 2012).

### 2.2.5. 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 & Merz, 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 and may even alarm-call (Goodall, 1986a; 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, in contrast to dead birds, they were more fearful of dead and seemingly dead mammals or mammal models (mangabey, goat, antelope) than 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 behavioral pattern possibly widespread among primates[14]. 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).

## 3. Evolutionary and Cognitive Aspects of Primate Thanatology

### 3.1. 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

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[14] Struhsaker (1967) also mentions in passing that a group of vervet monkeys ignored the recent carcass of a zebra fetus they passed by, even though it was a perfectly good source for nutritional value. Discussing data on chimpanzees and baboons, Ragir et al. (2000) make an interesting proposal that carrion avoidance in meat-eating in extant non-human primates and early hominins is a diatery stragegy developed throughout their lives as a response to potential gastrointestinal illnesses associated with the ingestion of contaminated meats.

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 color change (Stevens & Merilaita, 2009), or engage in behaviors such as freezing (Hagenaars, Oitzl, & Roelofs, 2014) or thanatosis (Humphreys & Ruxton, 2018).

In primates, life detection is arguably 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, I 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 specialized 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 behavior reading. This implies a reasoning involving little mental state attribution, focusing instead on behavioral 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 (Santos & Hauser, 1999; Phillips et al., 2009; 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 scrutinized through behavioral 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 endeavored 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 (Krupenye 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.

### 3.2. Levels of death awareness

Despite the abundance of multimodal cues that could potentially inform primates of death when they encounter it in novel situations (see Figure 5.6), 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 generalized threat detection mechanism. How would a concept such as ‘ex-agent’ emerge? I propose a three-level division of death cognizance which relates both to the cognitive/developmental and phylogenetic levels of the primate order.

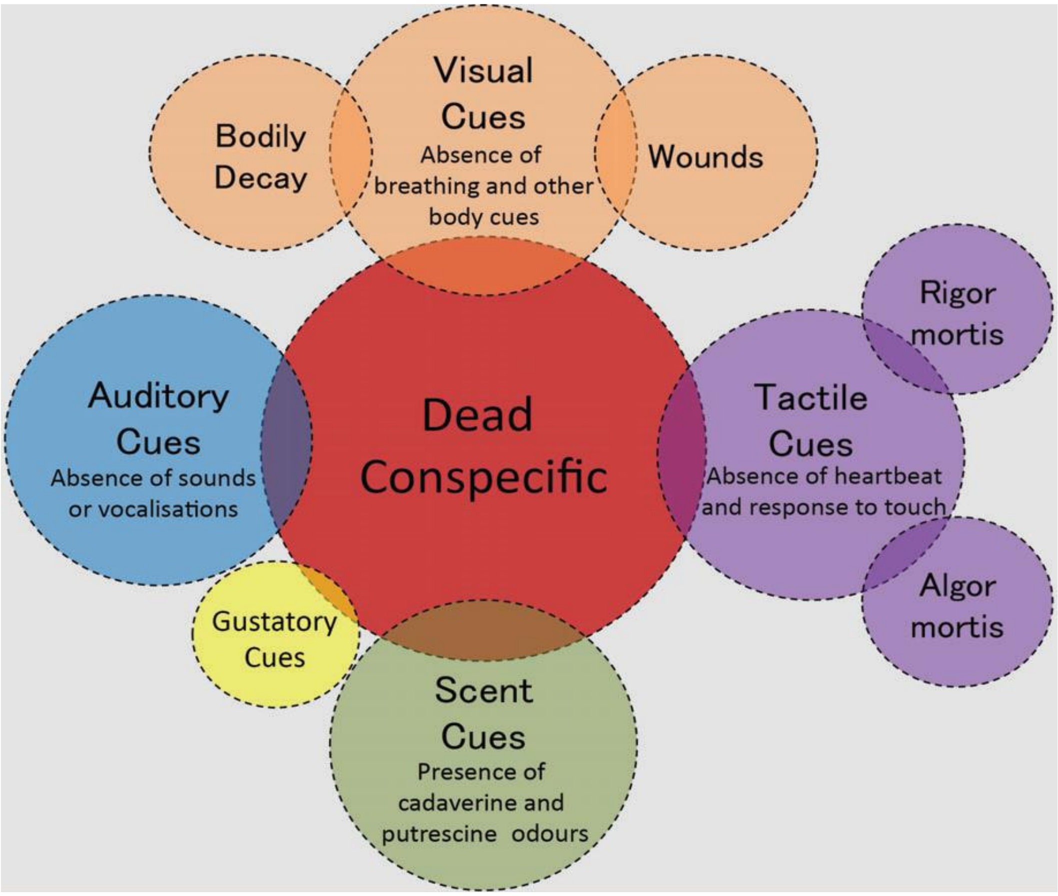

Figure 5.6. Sensory cues to death available to primates: a combination of the presence and absence of signals.

(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 an external force is applied. We know that monkeys recognize 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 & Gredeb¨ack, 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 nearly all animal 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 directs 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 threats (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-categorized as one that does neither). Observations on monkeys suggest that this re-categorization 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[15] – 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,

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[15] However there are challenges to this view when it comes to detecting so-called *secondary cues of danger*. Cheney and Seyfarth (1985) in a series of experiments designed to assess monkeys' knowledge (vervets and baboons) about dangerous cues to predators, found that in none of the instances did the experimental subjects react to an experimentally placed carcass or snake tracks. For instance, despite that it fooled one tour bus driver into thinking there was a leopard in the area when they placed a stuffed carcass of Thompson's gazelle on a tree (tree-hoisting is a typical caching behavior by leopards) in close proximity to the monkeys' sleeping site (4 groups of vervets and 1 of baboons). Observing their behavior for 2 hours upon reaching the carcass site, they noticed neither alarm calling nor increased vigilance for either monkey group and, for all intents and purposes, none acted as if they took notice that the carcass might indicate the presence of a leopard. Moreover, even though one vervet group had encountered a leopard in a tree with a carcass, and alarm-called continuously even when the leopard left the tree, this group too, showed no significant behavioral shift in their experiment. This contrasts with chimpanzee behavior, a connection noted previously by Hosaka et al. (2000) in which chimpanzees tend to alarm call at carcasses of conspecifics, a pattern also true for similar-sized heterospecifics (see Gonçalves & Carvalho, 2019).

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 1.2).

Table 1.2. Conceptual acquisition of death in humans*

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

*Speece & Brent (1996); Kenyon (2001); Longbottom & Slaughter (2018)

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 realize 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 about 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, 2005; Barrett & Behne, 2005). Their cessation of agency hypothesis (Barrett, 2005; Barrett & Behne, 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. 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-categorization 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 Tai 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-categorized 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. At 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). Kortlandt (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 (see Chapter 1, p15), 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) (see Figure 5.7). 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.

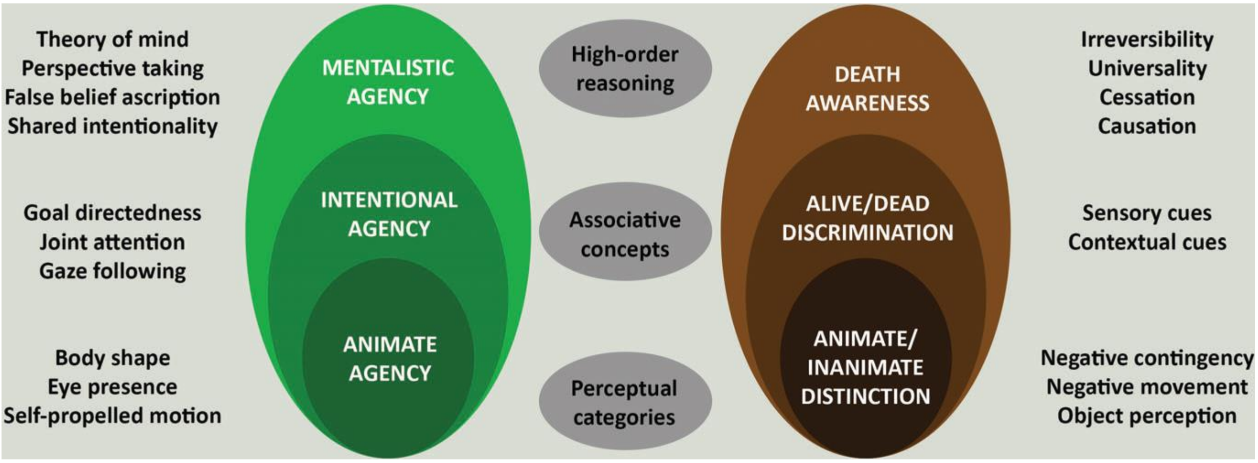

Figure 5.7. Integrated model of life–death awareness. The first levels are governed by perceptual categorisation, whilst the second and third levels are governed by associative concept learning and high-order reasoning (analogical/inductive/causal reasoning), respectively. Species possessing all these cognitive processes are in a likely position to acquire an emergent conceptual awareness of death.

### 3.3. Grief becomes mourning

Conjectures have been made regarding the thanatological behavior of extinct primates. Pettitt (2011), assessing data from chimpanzees, suggested that such behaviors 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 behavioral features that accompany it. The living primate species that engage most often in dead-infant carrying behavior are typically terrestrial and/or capable of bipedal carriage, implying that hominin lineages with brain capacities and structures 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 behaviors gradually gave way to more ritualized 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 behavior development: *core mortuary*, *archaic mortuary*, *modernizing mortuary*, *modern mortuary*, and *advanced mortuary*. The behaviors 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 behavior are characterized 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 *modernizing mortuary phase*. Boesch (2012) observed chimpanzee corpses in Tai 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 behaviors occurred in hominins due to the perishable nature of such materials. Nonetheless, this could account for the large gaps in the mortuary 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).

But 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 behavioral 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. The deliberate placing of corpses in 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 behavioral 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 the immediate family by decreasing inclusive fitness but would also impact the wider group. Functionally speaking, mourning ceremonies shorten the grieving process by allowing ritualized re-categorization 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, Radestad & 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, 1986a; Strum, 1987; Yang et al., 2016). However, their failure to engage in the more elaborate mortuary behaviors 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 behavioral innovations. Biological trends included bipedal specializations and increased brain size (from the 400 cm3 of Australopithecines to the roughly 1400 cm3 of Homo sapiens) but also cortical re-organization (increased dominance of the prefrontal regions) (Holloway, 2015). Behavioral advances included a flaked stone industry with increased technological complexity over time (Toth & Schick, 2018), the 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. In particular, dead-infant carrying behavior is explained by a combination of factors (at both proximate and ultimate causation levels) that permit its emergence but also impact its duration. These range from anatomical (handling and carriage abilities), physiological/ emotional (hormones and grief management) to perceptual/ cognitive (errormanagement strategy, infantile cues, learning to mother), life history (parity, experience, individual differences) and ecological (climate, terrestriality/arboreality) factors. 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, I suggest interactions with the dead: (i) promote more rapid re-categorisation from living to dead; (ii) decrease costly vigilance/caregiving behaviours; (iii) are crucial to the management of grieving responses; (iv) update individual position in the group hierarchy; and (v) 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, 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 (Wisman & Shrira, 2015; Sarabian & MacIntosh, 2016) 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.

# Section 3. Empirical explorations of death-related cues in chimpanzees

# Chapter 6. Chimpanzees’ attention towards conspecific skulls

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“*What goes on in the chimpanzee’s mind when they see such a sight in the forest? We are able to draw some conclusions based on their behavior when they encounter dead individuals, but deciphering their actual thoughts remains speculative*”

Christophe Boesch [Wild Cultures, 2012, commenting on a picture of a chimpanzee skull]

## 1. Introduction

Chimpanzees and elephants share some curious traits; they are large-brained, long-lived animals with prolonged development, live in complex societies, are capable of mirror self-recognition, and display protracted interest towards injured and dead conspecifics (Hart et al., 2008; Gonçalves & Carvalho, 2019). Behavioural responses such as physical manipulation of the corpse, vigils, and visitations are strikingly similar among these two taxa (Gonçalves & Biro, 2018). Non-human animal interest in skeletons is not reported in the literature apart from records of osteophagia mostly observed in ungulates where the targets typically include horns, hoofs, and long-bones, usually explained as a form of nutrient consumption (Hutson et al., 2013). Elephants appear to be unusual in showing extended attention to dead conspecifics long after they decompose, often interacting with their skeletons for protracted durations. However, there is one report of similar behavioural responses in bovids (*Bos javanicus*) to both conspecific and non-conspecific bones, though neither as marked nor as elaborate as seen in elephants (Halder & Schenkel, 1972).

### 1.1 Elephants: Observations & empirical research

Elephant post-mortem attentive behaviour has been documented in all three extant species of elephants (Douglas-Hamilton et al., 2006; Sharma et al., 2019; Howley et al., 2019). Long known to elephant researchers, interest in dead conspecifics is not only limited to carcasses but also extends toward conspecific bones and tusks (Goldenberg & Wittemeyer, 2020). During a study of elephant carcass decomposition, the skull was transported as far as 100m from the original site by other elephants (Coe, 1978). Noticing this natural propensity towards interaction with conspecific bones by wild African elephants, and inspired by Iain Douglas-Hamilton's so-called "crude experiments" three decades before (Douglas-Hamilton & Douglas-Hamilton, 1975), McComb, and colleagues (2006) devised an experiment to empirically measure how their interest contrasted with other objects placed in the environment. Their experiments consisted of systematically placing three objects in a line, 1m from each other, order randomized in each trial, and placed at 25-30 m from the nearest elephant group. The first condition consisted of an elephant skull, elephant tusk, and a piece of wood. Similarly, in the second condition, the skull of an elephant was presented alongside the skulls of a buffalo and a rhinoceros. Finally, the third condition comprised three skulls of elephant matriarchs, one of an individual known to the group while alive. Because olfaction is a substantial sensory domain in elephants, to control for smell, all bone stimuli were completely dried and treated. The results showed that elephants (i) approached and manipulated elephant tusks significantly more than other objects, (ii) similarly showed more interest in conspecific skulls than non-conspecific skulls, and (iii) appeared not to differentiate skulls of previously known individuals from the skulls of strangers. Their main findings are further supported by an informal experiment conducted by Goldenberg and Wittemeyer (2020) in which they presented elephant, giraffe, and Cape buffalo bones to wild elephants, with the most interest shown to elephant bones. Similar results were obtained in captive elephants (Rassmussen *in* Goldenberg & Wittemeyer, 2020).

### 1.2 Chimpanzees: Observations & empirical research

Two classic comparative psychology studies give us some insights into this topic regarding skeletons. First, Ladygina-Kohts (1935/2002) researched the comparative development of chimpanzees and humans. She presented her juvenile male chimpanzee (Joni) with an array of stimuli (dead hen/grouse, dead magpie, dead hare, monkey skeleton, human skull). His general response towards these objects was initially of fear and apprehension and then curiosity and excitement, touching them with his index finger and then smelling them. Second, Donald Hebb's seminal experiments on fear (Hebb, 1946), with thirty captive chimpanzees, involved presenting each of them with several "fear-inducing" stimuli (juvenile chimpanzee skull with a moveable jaw, chimpanzee death-mask, an infant chimpanzee corpse, etc.). While their responses were mostly fearful (Hebb's attempt to explain the underlying fear mechanisms initiated by these objects was his main contribution) the chimpanzees were also faced with objects showing conflicting perceptual cues leading to incompatibilities at the cognitive level (incomplete physical features and lack/presence of movement).

Several published reports describe chimpanzees' reactions towards their dead, ranging from affiliative to aggressive and from quiet/passive to loud/expressive (Teleki, 1973; Hosaka et al., 2000; Anderson et al., 2010; Cronin et al., 2011; Stewart et al., 2012; Boesch, 2012; van Leeuwen et al., 2016; Pruetz et al., 2017). Indeed, chimpanzee mothers have been observed carrying their dead infants for days, weeks, or months (Lonsdorf et al., 2020), a pattern commonly observed in many females across the primate order (Watson & Matsuzawa, 2018; Fernandez-Fueyo et al., 2021). While these publications have contributed to our knowledge of *Pan thanatology*, we still know very little about how chimpanzees engage with skeletons in their natural environments. Not many observations have been made of this phenomenon with one notable exception. Among many thanatological interactions in wild chimpanzees and gorillas, Watts (2020) recounts two cases where the Ngogo Community chimpanzees interacted with skeletonised conspecifics (retaining some hair and ligaments). In the first case, the chimpanzees stopped, looked vigilant, gave alarm calls, and clustered on the ground and in the trees around the chimpanzee skeleton, looked at it for around 5min and stayed at 3-4 m from it. In the second case, the chimpanzees clustered around the skeleton, peering at it for 2 min with many positioned 0.5 m from it, before departing. Aware of McComb's elephant study, Watts (2020) goes on to conjecture that skeletons capture attention because they still bear some "iconic resemblance" to living chimpanzees and that individuals may employ anatomical knowledge based on skeletons of prey species or perhaps in conjunction with the recognition of chimpanzee teeth or hair (when present in the skeleton). Notably, both deaths resulted from intra and inter-community killings, respectively, carried out by some of the chimpanzees involved in these interactions. Given the diversity of chimpanzees' thanatological responses (Anderson, 2018), we should be careful not to interpret these results conclusively as a general pattern, but rather integrate them within a wider range of possible chimpanzee responses to conspecific skeletons.

### 1.3 Face perception research

The literature on chimpanzees' responses towards their dead shows that they (and other non-human primates) pay substantial attention to the face, presumably due to its communicative value

(Gonçalves & Carvalho, 2019). Faces are an important category of visual stimuli for both humans and non-human animals as evidenced by several studies conducted on vertebrate species (Leopold & Rodes, 2010). They can provide information on identity (sex, age, rank), communicate many emotional expressions, and provide information on attentional states (gaze) and attraction (mate quality) (Adachi & Tomonaga, 2017). Comparative cognitive research on facial perception has hinted at a close relationship between humans and chimpanzees. Like humans, chimpanzees show similar responses to faces, for example, rapid individuation of faces, conspecific face-inversion effects, and second-order relational information (Parr, 2011). This should not be surprising since there was likely a strong evolutionary pressure for attending to faces in primates (and other taxa), since faces carry all sorts of advantageous information (conspecific vs non-conspecific, in-group vs out-group member, threat vs non-threat, etc.). In non-human primates, such face-to-face interactions start from birth with these experiences shaping their brain activity and guiding their knowledge of socially appropriate behaviours continuously throughout life (Kuwahata et al., 2004; Vandewert et al., 2015).

Research into human face perception accounted for distinct levels of configural/holistic processing since faces carry specific information: *first-order relational properties* (i.e. arrangement of facial features: eyes above the nose, nose above the mouth, allowing us to detect a face), *second-order relational properties* (i.e. variation in such facial arrangement, allowing us to discriminate between individual faces: spacing and positioning of eyes, mouth, nose) (Piepers & Robbins, 2012). Many hypotheses have been put forth to explain this general propensity to attend to faces, one such involves an innate processing module followed by a learning module (Morton & Johnson, 1991). While there is debate as to which precise aspects are innate *versus* learned, general support for both has been shown both in the human and comparative literature (Sugita, 2008; Parr, 2011).

### 1.4 Research motivations & questions

I began this study with the assumption that chimpanzee skulls are perceived much like chimpanzee faces and, likewise, would be subjected to identical attentional biases. With different sets of stimuli, controlled for size, in hypothesis 1a, I predicted that chimpanzees would show a conspecific bias that would be stronger for faces, followed by skulls, and finally stones. Moreover, assuming such interest is guided by some sort of face-like recognition (i.e. configural facial/face-like arrangements and outlines), in hypothesis 1b I predicted that chimpanzees would exhibit longer looking times and patterns towards conspecific frontal-facing and diagonally-presented stimuli, but to a lesser extent for laterally presented stimuli. Moreover, in hypothesis 2, I predicted that chimpanzees would show a preference for chimpanzee faces over chimpanzee skulls and the outlines of skulls (filled with stone textures). Finally, because elephants show significant interest towards tusks, perhaps by association (tusks are visible, salient, body parts in live conspecifics), likewise in hypothesis 3 I predicted that chimpanzees would direct their attention most prominently towards the teeth as proposed by Watts (2020) (see Figure 6.1).

Despite the intriguing findings, McComb and colleagues' study was not without limitations. For instance, they could not control for parameters such as size, colour, or luminance. While the latter two might not be critical to their experiment given elephants' poorer visual acuity in comparison to chimpanzees' (Bard et al., 1995; Pettigrew et al., 2010), the fact that an elephant skull is roughly twice the size of a rhinoceros or a hippopotamus skull remains somewhat more problematic.

Because chimpanzees are predominantly visual, to answer these questions I devised an experiment showing them images, controlled for size and luminance, and measured their differential looking times using an eye-tracking device.

**Hypothesis 1a**: Chimpanzees prefer chimp face-like stimuli (face, skull, stone) over other species facial stimuli
**Hypothesis 1b**: This effect is stronger in frontal compared to lateral orientations

**Hypothesis 2**: Chimpanzees prefer chimpanzee faces over chimpanzee skulls and chimpanzee-shaped stones respectively

**Hypothesis 3:** Chimpanzees show preference for teeth (recognisable cue in live chimpanzees) in chimpanzee skulls over other areas (eye and nasal cavity regions)

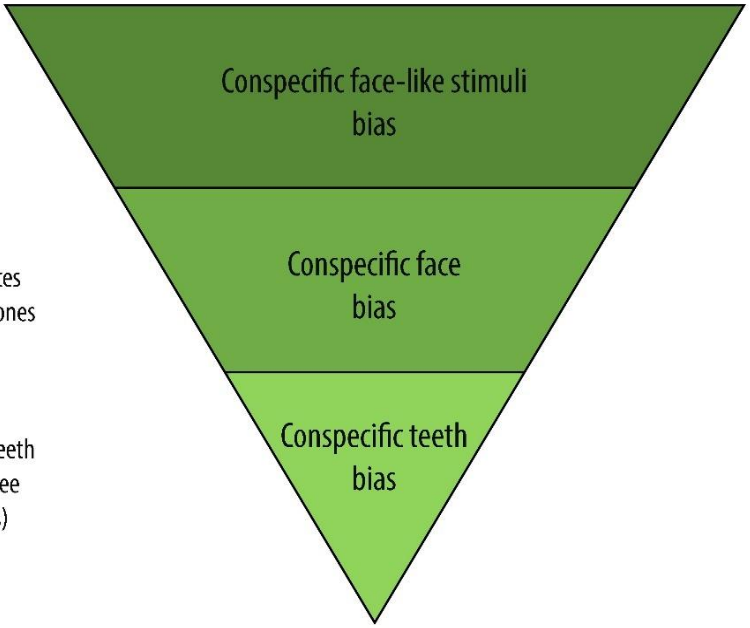

Figure 6.1. Diagram illustrating the hypotheses from the general (conspecific stimuli), the central (conspecific face) to the narrow. (conspecific teeth).

## 2.Materials and Methods

### 2.1 Subjects

The experiment initially included ten adult chimpanzees (*Pan troglodytes*), with three subsequent dropouts[16] reducing the total to seven subjects (three males and four females). All

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[16] These dropouts were due to different causes (neurological, physical, and temperamental) which affected the completion of the sessions. One chimpanzee (Pendesa) exhibited erratic visual patterns – she suffers from an arachnoid cyst in her brain which seems to have partially affected her visual field (see Kaneko et al., 2013). Another subject (Mari) has difficulty breathing through her nose which affected her

individuals were housed at the Primate Research Institute, Kyoto University, Japan. These individuals were members of two social groups (totalling 11) living in an environmentally enriched facility comprising two outdoor enclosures (250 m$^2$ and 280 m$^2$), an open-air outdoor enclosure with vegetation and climbing structures (700 m$^2$), and indoor living rooms linked to the testing rooms (Ochiai & Matsuzawa, 1999). They had access to water *ad libitum* and received a variety of foods several times a day. All research procedures followed institutional guidelines (Primate Research Institute 2010 version of 'The Guidelines for the Care and Use of Laboratory Primates') and the experimental protocol was approved by the Animal Welfare and Animal Care Committee of the Primate Research Institute and the Animal Research Committee of Kyoto University.

## 2.2 Apparatus

This research was conducted in an experimental booth (1.80 × 2.15 × 1.75 m) inside a testing room. Each chimpanzee voluntarily walked to the booth through an overhead walkway connected to the indoor rooms and outdoor enclosures. I used a Tobii eye tracker (60 Hz; X300; Tobii Technology AB, Stockholm, Sweden). Sets of images were shown at a resolution of 1280x720 pixels on a 23-inch LCD monitor (ca. 43x24 degree) using TobiiStudio software (v. 3.2.1.) at approx. 60 cm. Both the eye-tracking device and the monitor were outside the experimental booth, the subject's eye movements being recorded through a transparent acrylic panel (1 cm thick). To reduce head movements during stimulus presentation, the subjects were able to sip juice through a nozzle and tube attached through a hole in the acrylic panel (see Figure 2). At the beginning of

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comfort sipping the juice resulting in her ceasing the experiment altogether. The third (Pan), would for no apparent reason (without any overt signs of disgust or distress) abandon the experiment midway through or not come at all despite our best attempts to entice her.

each test session, automated calibrations were conducted for each subject, these involved one small clip of a stirring object presented twice on each opposing corner of the screen. Following these measures, calibration errors were typically within one degree (Kano & Tomonaga, 2011).

## 2.3. Procedure & Stimuli

For experiment 1, I presented a total of 180 images to the chimpanzees (4 species x 3 types (material) x 3 angles x 5 image variations). Each image group comprised four species (cat, chimp, dog, and rat) shown simultaneously at each corner of the screen (Figure 6.2). Each image group consisted of one of three types (either skull, face, or skull-shaped stone). Moreover, each of these conditions was presented in three different orientations (diagonal, frontal, and lateral) (Figure 6.3).

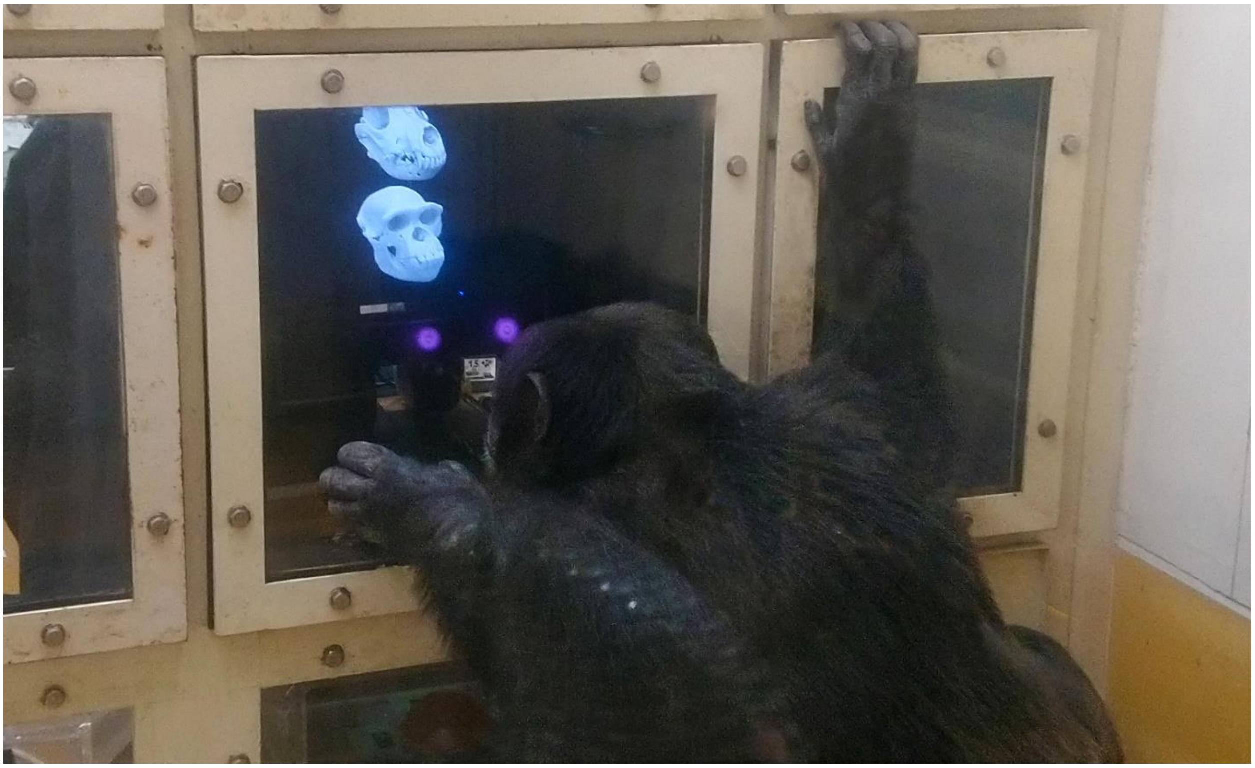


Figure 6.2. One test subject (Ayumu) performing an eye-tracking session in the experimental booth.

There were five variations per image within image groups (i.e. five different chimpanzee skulls presented in frontal, diagonal, and lateral orientations across five different sessions).

No images were repeated. These were controlled for size on Photoshop CS and averaged for luminance using Matlab 2018a with the ShineToolbox 1.2. package (Willenbockel et al., 2010). Each image group was presented for six seconds and looking durations were measured. To control for potential matching between image groups (presence of teeth in both faces and skulls), all faces depicted neutral expressions. Stones were geometrically manipulated into the outline of skulls. Due to the similarity of the stimuli, to avoid image fatigue, face and skull conditions were presented on different days together with the stone condition with a total of eight trials (one trial per day). I chose these three additional species since they are fairly common but also fairly distinct

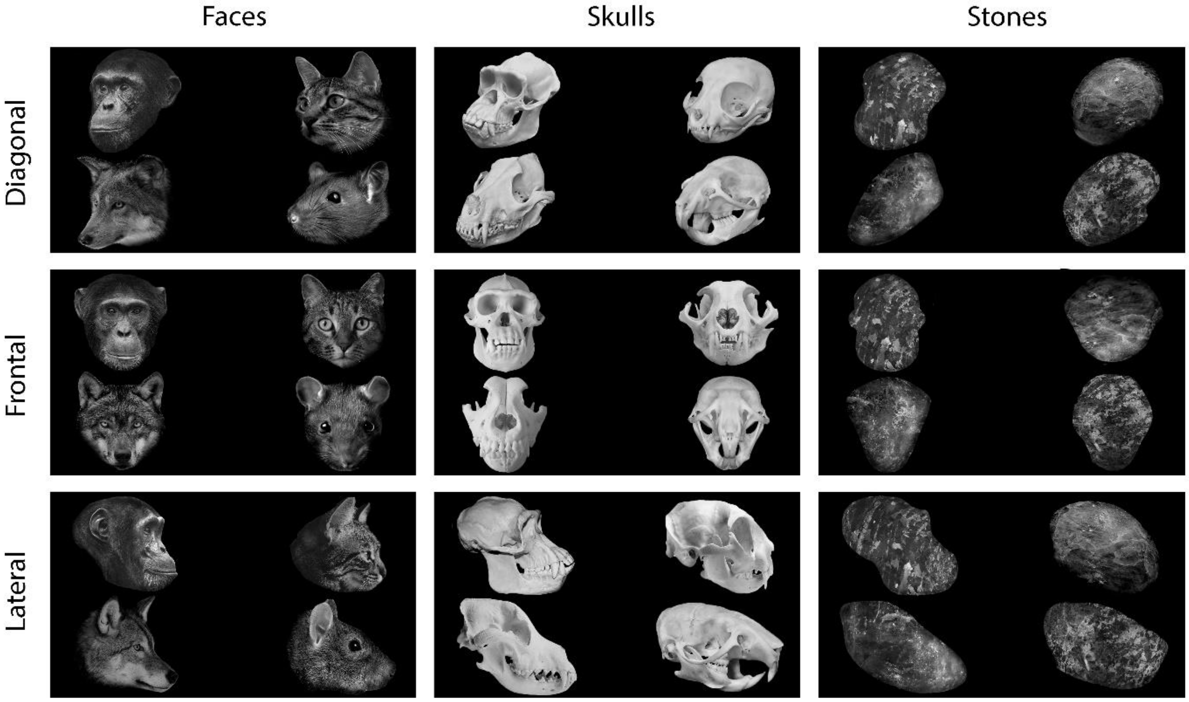


Figure 6.3. Examples of each image group stimuli presented to the chimpanzees (actual locations were randomized to avoid positional bias).

from each other. Apart from conspecific stimuli, the subjects were not overly familiar with the animal species presented, though they have seen both live and dead rodents (mice) and, to a lesser extent, live cats and dogs. None of them had any previous experience with skulls of any type. Each image-group was presented for 6 seconds and was followed by a fixation cross at the middle. On each stimulus image (i.e. skull/face/stone) I drew areas of interest (AOIs) for each of the four species. These AOIs were slightly larger (10-15%) than the original stimuli to account for possible fixation errors. For experiment 2, I presented only the chimpanzee stimuli used in the previous experiment with all three types (face, skull, stone), generating a total of 45 images to the chimpanzees (1 species x 3 types x 3 angles x 5 image variations). Each image group was presented again for six seconds for a total of five separate sessions. Three AOIs were likewise drawn around the image stimuli as with experiment 1. Each image-group was presented for 6 seconds and followed by a fixation cross at the middle. For experiment 3, I presented only the chimpanzee skulls used in experiments 1 and 2 at the frontal and diagonal orientations, a total of 10 images. Because chimpanzees have forward-facing eyes, this perceptual feature is lost when both faces and skulls are presented sideways on, I did not include the lateral orientations in this experiment. Three AOIs were drawn around the eye socket, the nasal cavity, and the teeth regions. The AOIs were of equal size for teeth and eye regions and roughly half for the nasal cavity. Each image was presented for 5 seconds and followed by a fixation cross randomly at each corner of the screen. For all experiments, eye movement data were filtered using a Tobii fixation filter. As our looking time measure, I used the total fixation duration measurement generated by the Tobii Studio software. Total fixation duration is the sum of the duration of all fixations (in seconds) occurring during stimulus presentation (see Figure 6.4 for an overview of the experimental flow).

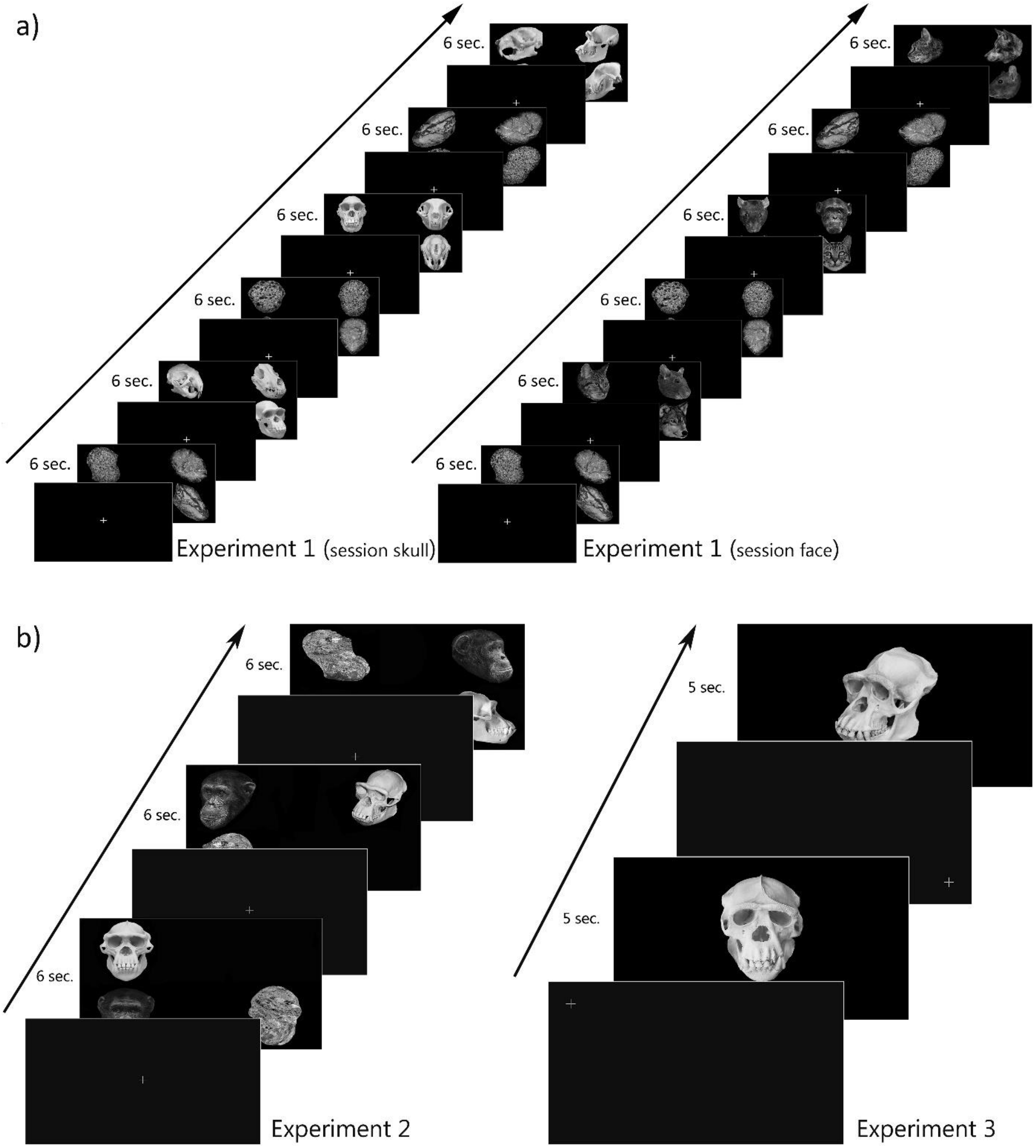


Figure 6.4. Experimental design flow for all three experiments.

## 2.4. Statistical Analysis

For the first experiment (conspecific stimuli bias), I presented five variations of image-group, then averaged the total fixation data by species accordingly (i.e. frontal skulls x 5 sessions, frontal faces x 5 sessions, frontal stones x 5 sessions). To detect any viewing preferences, I conducted a general linear mixed model (GLMM). I conducted three independent (GLMM) tests for each orientation (frontal, diagonal, and lateral). For the analyses, I set “species” (chimp, cat, dog, rat) and “type” (skull, face, stone) as within-subject factors, “gaze” (total fixation duration) as a dependent variable with “subject” (chimpanzee participants) nested in “trial” as random factors.

For the second experiment (conspecific face bias), I presented all chimpanzee stimuli simultaneously at each of the three orientations (i.e. frontal face + frontal skull + frontal stone) for five sessions. A GLMM was also conducted with all three orientations pooled with “gaze” as dependent variable, “type” as within-subject factor, and “subject” nested in “trial” as random factors.

For the third experiment (conspecific teeth bias), to determine where chimpanzees fixated their gaze in chimpanzee skulls, I presented chimpanzee skull images from both the frontal and diagonal orientations one image at a time at the centre of the screen for five sessions. A GLMM was conducted with the frontal and diagonal orientations pooled, “gaze” as dependent variable “type” (eye socket, nasal, and teeth regions) as within-subject factors and “subject” nested in “trial” as random factors.

Since our data was both zero-inflated and continuous, all statistical analyses were conducted on the package glmmTMB (Magnusson et al., 2017) with the ziGamma family and the log link function (full model results in Supplementary Data). The DHARMa package (Hartig, 2017) was used to assess for inflation and dispersion. Significance for whole model terms was assessed with the "drop1" function. *Post hoc* pairwise Bonferroni-corrected comparisons among levels (species and/or type) were conducted using the emmeans package. All analyses were conducted on R 4.1.0. (R Core Team, 2018).

# 3. Results

## 3.1 Experiment 1: Conspecific *versus* Heterospecific Stimuli (Faces, Skulls, Stones)

### 3.1.1 Frontal condition

In the frontal condition, (observations, N=420) there was a significant interaction between species and type ($\chi 2$=14.39, df=6, *p*=0.025). In the skull sub-condition chimpanzees looked longer overall at the *chimpanzee skulls* than for other species skulls. The following *post hoc* tests revealed this difference in fixation durations to be significant; *chimp/cat* (t=-3.81, *p*=0.0009), *chimp/dog* (t=3.64, *p*=0.0018), *chimp/rat* (t=4.48, *p*=0.0001). For the face sub-condition fixations were again longer for the chimpanzee stimuli than for other species and these differences were significant; *chimp/cat* (t=-5.871, *p*<.0001), *chimp/dog* (t=3.43, *p*=0.0039), *chimp/rat* (t=3.22, *p*=0.0083). Finally, for the stone sub-condition, looking durations were longer for the chimpanzee stimuli in comparison with other species, but these differences were nonsignificant, except for the dog: *chimp/cat* (t=-2.02, *p*=0.261), *chimp/dog* (t=2.96, *p*=0.019), *chimp/rat* (t=1.03, *p*=1) (see Table 1 and Figure 6.5).

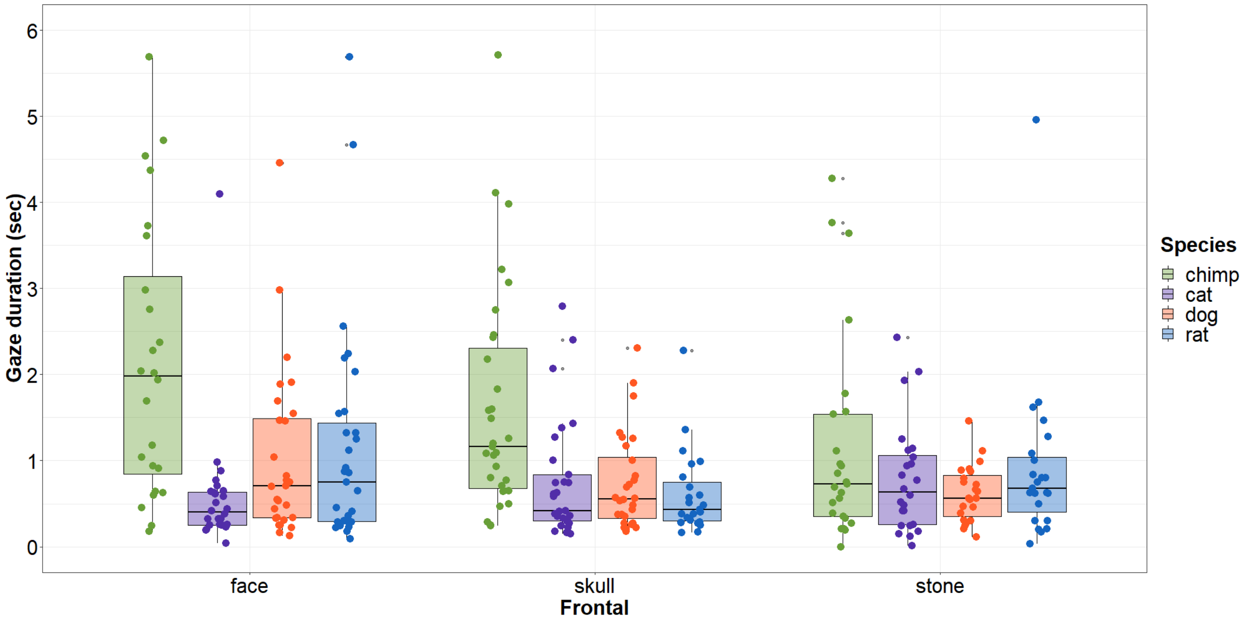
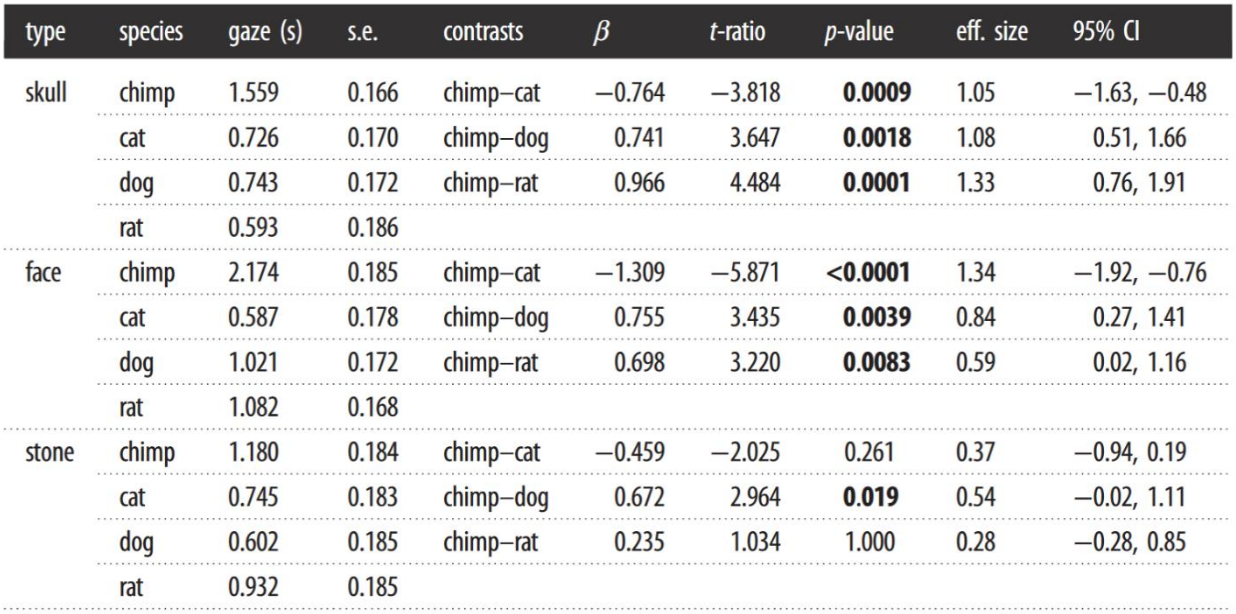


Figure 6.5.. Looking duration values for the frontal condition. Each dot represents a single individual's trial.

**Table 1.** Fixation duration results per species and type for the frontal condition. Significant results shown in bold.



| type | species | gaze (s) | s.e. | contrasts | *β* | *t*-ratio | *p*-value | eff. size | 95% CI |
|---|---|---|---|---|---|---|---|---|---|
| skull | chimp | 1.559 | 0.166 | chimp–cat | −0.764 | −3.818 | **0.0009** | 1.05 | −1.63, −0.48 |
| | cat | 0.726 | 0.170 | chimp–dog | 0.741 | 3.647 | **0.0018** | 1.08 | 0.51, 1.66 |
| | dog | 0.743 | 0.172 | chimp–rat | 0.966 | 4.484 | **0.0001** | 1.33 | 0.76, 1.91 |
| | rat | 0.593 | 0.186 | | | | | | |
| face | chimp | 2.174 | 0.185 | chimp–cat | −1.309 | −5.871 | **<0.0001** | 1.34 | −1.92, −0.76 |
| | cat | 0.587 | 0.178 | chimp–dog | 0.755 | 3.435 | **0.0039** | 0.84 | 0.27, 1.41 |
| | dog | 1.021 | 0.172 | chimp–rat | 0.698 | 3.220 | **0.0083** | 0.59 | 0.02, 1.16 |
| | rat | 1.082 | 0.168 | | | | | | |
| stone | chimp | 1.180 | 0.184 | chimp–cat | −0.459 | −2.025 | 0.261 | 0.37 | −0.94, 0.19 |
| | cat | 0.745 | 0.183 | chimp–dog | 0.672 | 2.964 | **0.019** | 0.54 | −0.02, 1.11 |
| | dog | 0.602 | 0.185 | chimp–rat | 0.235 | 1.034 | 1.000 | 0.28 | −0.28, 0.85 |
| | rat | 0.932 | 0.185 | | | | | | |

### 3.1.2 Diagonal condition

In the diagonal condition, (observations, N=420) I again found a significant interaction between species and type ($\chi 2$=50.21, df=6, *p*<.0001). In the skull sub-condition, while chimpanzees looked longer at the *chimpanzee skull* overall, the *post hoc* tests revealed that it was the comparison with the *dog skull* that drove the differences in fixation durations, with this difference significant; *chimp/cat* (t=-0.37, *p*=1), *chimp/dog* (t=3.26, *p*=0.007), *chimp/rat* (t=1.42, *p*=0.931). In the face sub-condition, the *post hoc* tests revealed that fixations were higher for the *chimp face versus* other species, with all differences significant; *chimp/cat* (t=-6.92, *p*<.0001); *chimp/dog* (t=5.39, *p*<.0001), *chimp/rat* (t=5.56, *p*<.0001). Lastly, in the stone sub-condition, the *post hoc* tests revealed no significant effects among species, excepting the cat which had longer looking durations compared to the chimpanzee;  *chimp/cat* (t=2.93, *p*=0.021), *chimp/dog* (t=-1.24, *p*=1), *chimp/rat* (t=1.03, *p*=1) (see Table 2 and Figure 6.6).

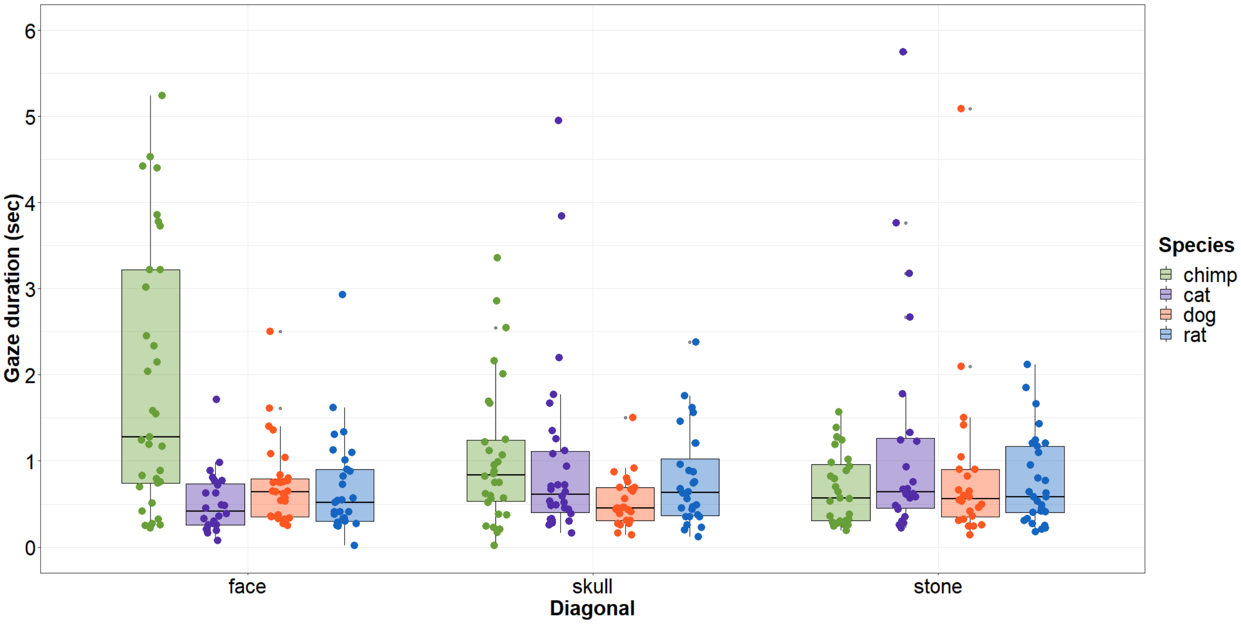
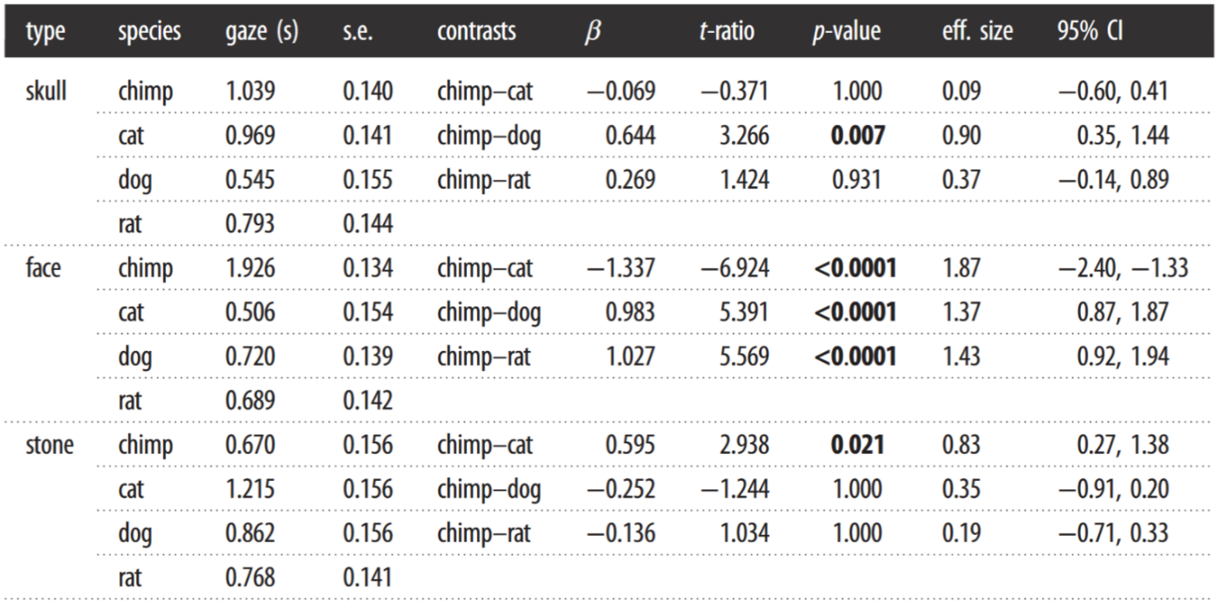


Figure 6.6. Looking duration values for the diagonal condition. Each dot represents a single individual's trial.

**Table 2.** Fixation duration results per species and type for the diagonal condition. Significant results shown in bold.



| type | species | gaze (s) | s.e. | contrasts | $\beta$ | $t$-ratio | $p$-value | eff. size | 95% CI |
|---|---|---|---|---|---|---|---|---|---|
| skull | chimp | 1.039 | 0.140 | chimp–cat | −0.069 | −0.371 | 1.000 | 0.09 | −0.60, 0.41 |
| | cat | 0.969 | 0.141 | chimp–dog | 0.644 | 3.266 | **0.007** | 0.90 | 0.35, 1.44 |
| | dog | 0.545 | 0.155 | chimp–rat | 0.269 | 1.424 | 0.931 | 0.37 | −0.14, 0.89 |
| | rat | 0.793 | 0.144 | | | | | | |
| face | chimp | 1.926 | 0.134 | chimp–cat | −1.337 | −6.924 | **<0.0001** | 1.87 | −2.40, −1.33 |
| | cat | 0.506 | 0.154 | chimp–dog | 0.983 | 5.391 | **<0.0001** | 1.37 | 0.87, 1.87 |
| | dog | 0.720 | 0.139 | chimp–rat | 1.027 | 5.569 | **<0.0001** | 1.43 | 0.92, 1.94 |
| | rat | 0.689 | 0.142 | | | | | | |
| stone | chimp | 0.670 | 0.156 | chimp–cat | 0.595 | 2.938 | **0.021** | 0.83 | 0.27, 1.38 |
| | cat | 1.215 | 0.156 | chimp–dog | −0.252 | −1.244 | 1.000 | 0.35 | −0.91, 0.20 |
| | dog | 0.862 | 0.156 | chimp–rat | −0.136 | 1.034 | 1.000 | 0.19 | −0.71, 0.33 |
| | rat | 0.768 | 0.141 | | | | | | |

### 3.1.3 Lateral condition

In the lateral condition, (observations, N=420) I found, yet again, significant interactions between species and type, ($\chi 2$= 14.02, df=6, $p$=0.0293). The following *post hoc* tests in the skull sub-condition, revealed no significant differences in fixation durations where *chimpanzee skulls* were compared: *chimp/cat* (t=-1.46, $p$=0.856), *chimp/dog* (t=1.94, $p$=0.311), *chimp/rat* (t=-1.48, $p$=0.823). Unexpectedly, chimpanzees looked longer at *rat skulls* overall and, significantly so when compared to *cat* and *dog skulls*. To further explore this effect, a follow-up lateral test was conducted with the rat skull's diastema covered. The previous significant results were no longer found in the follow-up test, although there was an overall higher trend for *chimpanzee skulls* (see Section 5.1 and Supplementary Data). In the face sub-condition fixations were longer for the chimpanzee stimuli than for other species and these differences were significant when compared to *cat* and *dog skulls*; *chimp/cat* (t=-2.69, $p$=0.044), *chimp/dog* (t=2.26, $p$=0.143), *chimp/rat* (t=2.78, *p*=0.034). For the stone sub-condition, looking durations were slightly longer for the chimpanzee stimuli in comparison with other species, however, these differences were nonsignificant: *chimp/cat* (t=-0.85, *p*=1), *chimp/dog* (t=2.01, *p*=0.268), *chimp/rat* (t=1.24, *p*=1) (see Table 3 and Figure 6.7).

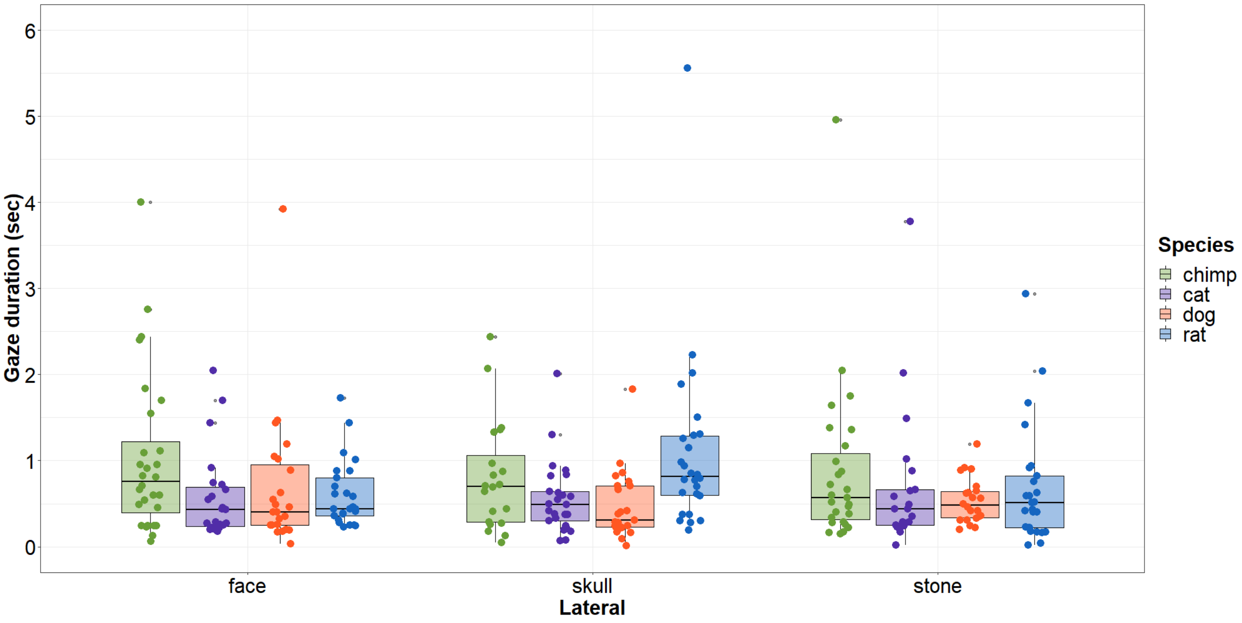


Figure 6.7. Looking duration values for the lateral condition. Each dot represents a single individual's trial.

**Table 3.** Fixation duration results per species and type for the lateral condition. Significant results shown in bold.

| type | species | gaze (s) | s.e. | contrasts | *β* | *t*-ratio | *p*-value | eff. size | 95% CI |
|---|---|---|---|---|---|---|---|---|---|
| skull | chimp | 0.766 | 0.185 | chimp–cat | −0.340 | −1.469 | 0.856 | 0.44 | −1.04, 0.15 |
| | cat | 0.545 | 0.167 | chimp–dog | 0.463 | 1.949 | 0.311 | 0.60 | −0.006, 1.22 |
| | dog | 0.482 | 0.176 | chimp–rat | −0.343 | −1.489 | 0.823 | 0.45 | −1.04, 0.14 |
| | rat | 1.080 | 0.164 | | | | | | |
| face | chimp | 1.063 | 0.161 | chimp–cat | −0.591 | −2.696 | **0.044** | 0.77 | −1.34, −0.20 |
| | cat | 0.588 | 0.177 | chimp–dog | 0.505 | 2.267 | 0.143 | 0.66 | 0.08, 1.24 |
| | dog | 0.641 | 0.177 | chimp–rat | 0.593 | 2.780 | **0.034** | 0.78 | 0.22, 1.33 |
| | rat | 0.587 | 0.166 | | | | | | |
| stone | chimp | 0.852 | 0.162 | chimp–cat | −0.194 | −0.854 | 1.000 | 0.25 | −0.84, 0.33 |
| | cat | 0.701 | 0.182 | chimp–dog | 0.448 | 2.013 | 0.268 | 0.58 | 0.01, 1.16 |
| | dog | 0.544 | 0.176 | chimp–rat | 0.268 | 1.241 | 1.000 | 0.35 | −0.20, 0.91 |
| | rat | 0.651 | 0.169 | | | | | | |

### 3.2 Experiment 2: Conspecific Stimuly (Faces with Skulls & Stones)

For experiment 2, (observations, N=315) with orientations now pooled, there was a significant effect among chimpanzee types (face, skull, stone) ($\chi 2$= 39.11, df=2, *p<.0001*). The results show that *chimpanzee faces* had the highest looking durations, followed by *chimpanzee skulls* and lastly *chimpanzee-shaped stones*. The following *post hoc* tests revealed that fixation durations, were significantly longer for the *chimpanzee face* in comparison to *skull* and *stone* types, but not when *skull* and *stone* were compared with each other; *face/skull* (t=4.04, *p*=0.0002), *face/stone* (t=6.34, *p*<.0001), *skull/stone* (t=2.26, *p*=0.073). (see Table 4 and Figure 6.8).

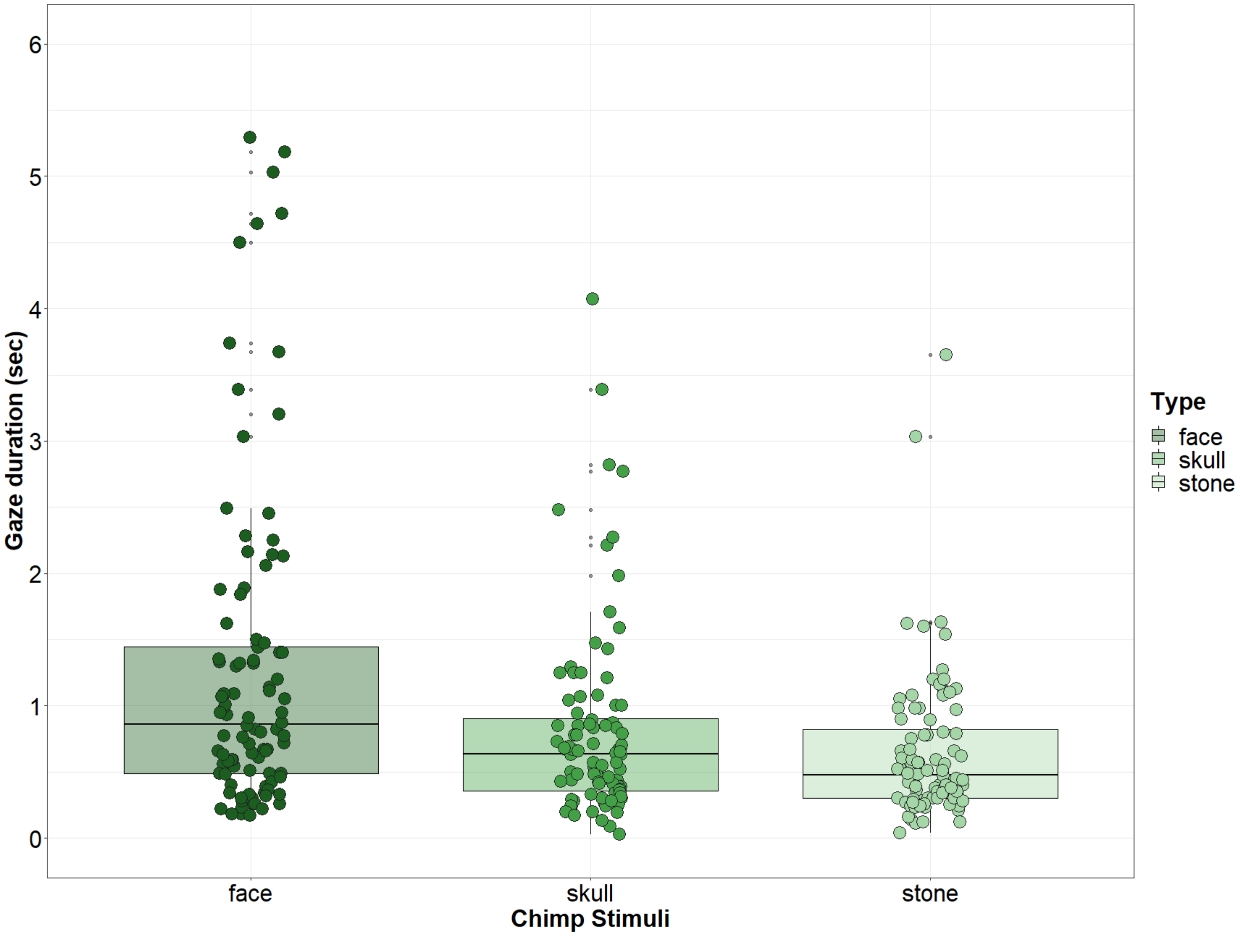
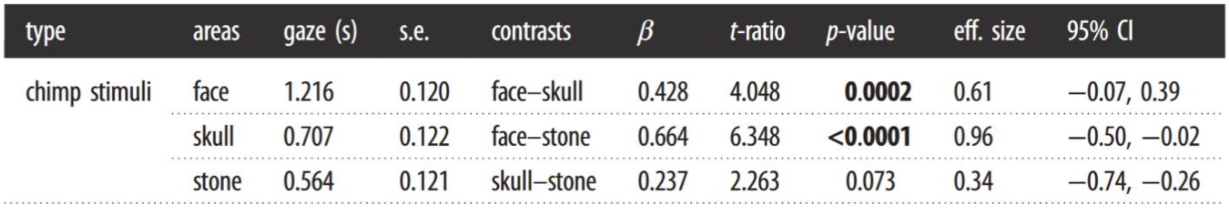


Figure 6.8. Looking duration values for the chimpanzee-only stimuli. Each dot represents a single individual's trial.

### 3.3 Experiment 3: Conspecific Skull Regions (Eye, Nasal & Teeth Regions)

For experiment 3, (observations, N=210) I found a significant effect among the chimpanzee skull AOIs (eye, nasal, and teeth regions) ($\chi 2 = 24.73$, df=2, $p<.0001$). The *post hoc* tests revealed the longer fixations for *teeth* compared to the *eye* and *nasal* regions to be significantly different, whereas the relationship between eyes and nose was non-significant: *eyes/teeth* (t=-4.25, *p*=0.0001), *nose/teeth* (t=-4.42, *p*<.0001), *eyes/nose* (t=0.20, *p*=1) (see Table 5 and Figure 6.9).

**Table 4.** Fixation duration results for the chimpanzee stimuli. Significant results shown in bold.



| type | areas | gaze (s) | s.e. | contrasts | $\beta$ | *t*-ratio | *p*-value | eff. size | 95% CI |
|---|---|---|---|---|---|---|---|---|---|
| chimp stimuli | face | 1.216 | 0.120 | face–skull | 0.428 | 4.048 | **0.0002** | 0.61 | −0.07, 0.39 |
| | skull | 0.707 | 0.122 | face–stone | 0.664 | 6.348 | **<0.0001** | 0.96 | −0.50, −0.02 |
| | stone | 0.564 | 0.121 | skull–stone | 0.237 | 2.263 | 0.073 | 0.34 | −0.74, −0.26 |

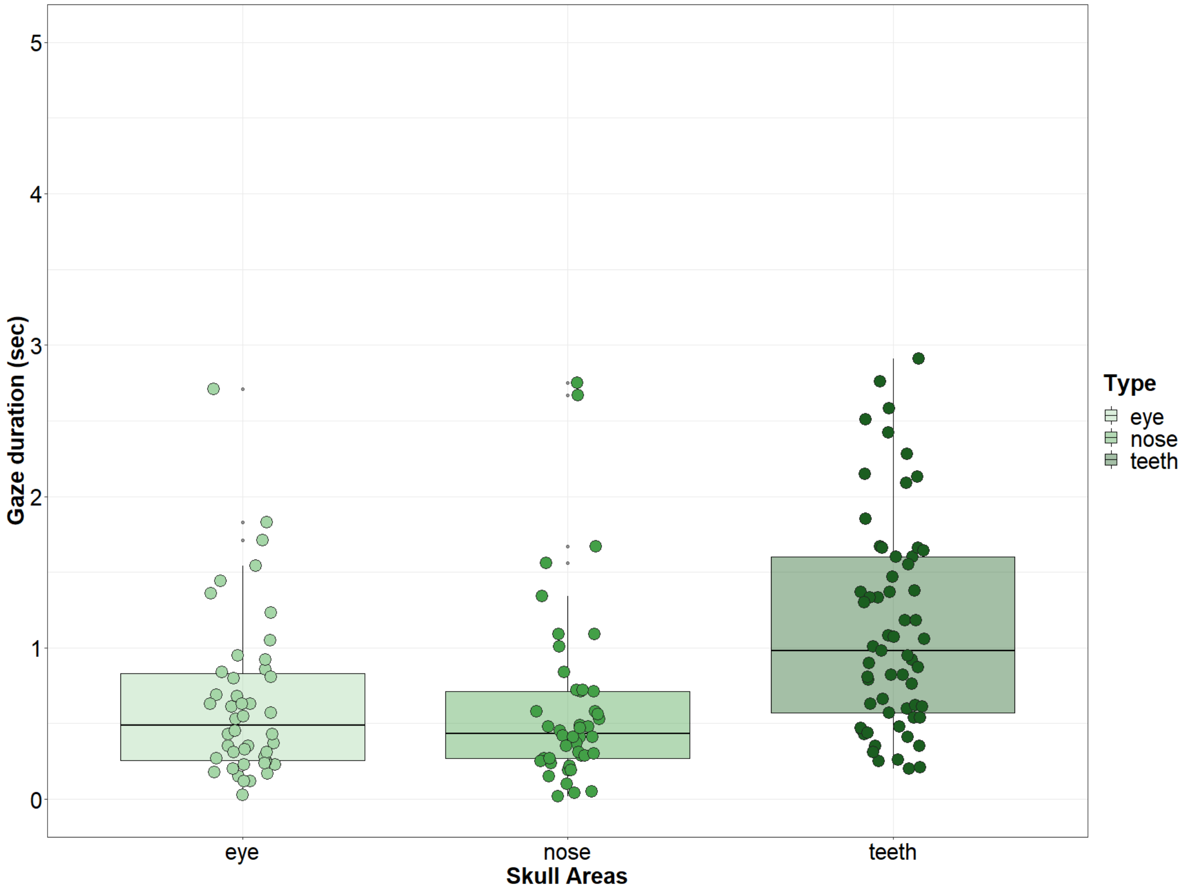
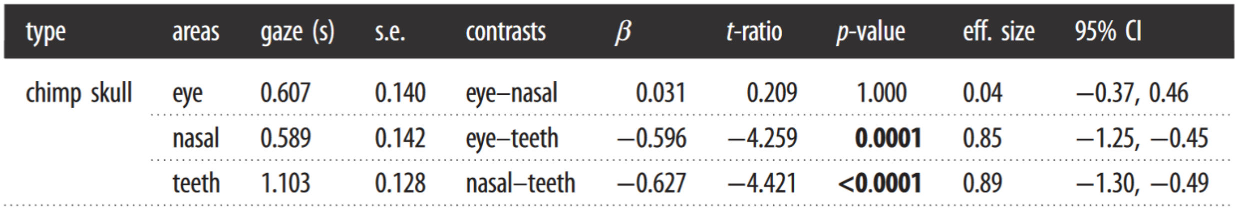


Figure 6.9. Looking duration values for the chimpanzee regions of the skull. Each dot represents a single individual's trial.

**Table 5.** Fixation duration results for the chimpanzee skull regions. Significant results shown in bold.



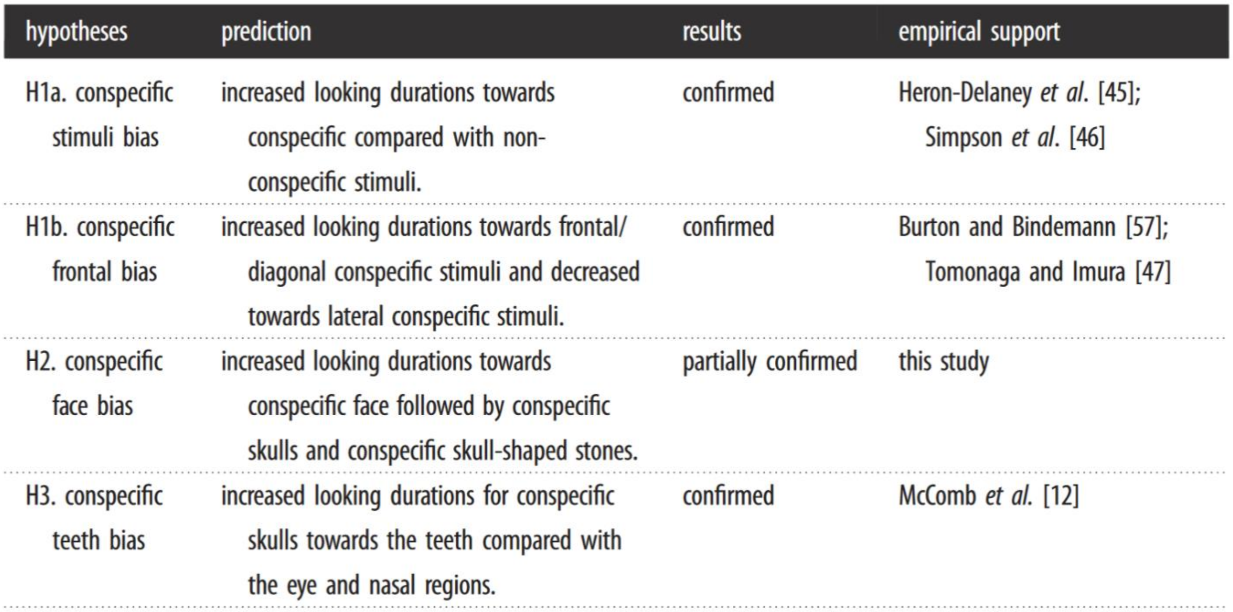
| type | areas | gaze (s) | s.e. | contrasts | $\beta$ | *t*-ratio | *p*-value | eff. size | 95% CI |
|---|---|---|---|---|---|---|---|---|---|
| chimp skull | eye | 0.607 | 0.140 | eye–nasal | 0.031 | 0.209 | 1.000 | 0.04 | −0.37, 0.46 |
| | nasal | 0.589 | 0.142 | eye–teeth | −0.596 | −4.259 | **0.0001** | 0.85 | −1.25, −0.45 |
| | teeth | 1.103 | 0.128 | nasal–teeth | −0.627 | −4.421 | **<0.0001** | 0.89 | −1.30, −0.49 |

# 4. Discussion

## 4.3. General Findings

Our primary aim was to find out if chimpanzees treat skulls similarly to faces (presumably via activation of a face module) and draw attention to the implications for comparative thanatology research where corpses in advanced states of decay and skeletons are involved. In the first experiment, with hypothesis 1a I wanted to determine if chimpanzees were relatively more interested in conspecific stimuli and with hypothesis 1b to see if such interest would also have an orientation-effect, with a preference for frontal and diagonal over lateral orientations expected. In the second experiment, with hypothesis 2 I sought to ascertain whether chimpanzee faces were the driving factor guiding our subject's attention when these were placed with chimpanzee skulls and stones. Finally, in the third experiment, with hypothesis 3, I needed to uncover whether such attention was concentrated on cues naturally visible in faces, in this case, teeth. The results show that they do but in a restricted sense. Overall, our subjects showed the most interest in conspecific faces, followed by conspecific skulls, and the least interest in conspecific skull-shaped stones. Moreover, this was particularly evident in frontal/diagonal orientations for chimpanzee faces and skulls. Furthermore, chimpanzees showed interest in conspecific teeth only relative to the eye and nasal regions of the skull (see table 6).

**Table 6.** Research hypotheses and results.



| hypotheses | prediction | results | empirical support |
|---|---|---|---|
| H1a. conspecific stimuli bias | increased looking durations towards conspecific compared with non-conspecific stimuli. | confirmed | Heron-Delaney *et al.* [45]; Simpson *et al.* [46] |
| H1b. conspecific frontal bias | increased looking durations towards frontal/diagonal conspecific stimuli and decreased towards lateral conspecific stimuli. | confirmed | Burton and Bindemann [57]; Tomonaga and Imura [47] |
| H2. conspecific face bias | increased looking durations towards conspecific face followed by conspecific skulls and conspecific skull-shaped stones. | partially confirmed | this study |
| H3. conspecific teeth bias | increased looking durations for conspecific skulls towards the teeth compared with the eye and nasal regions. | confirmed | McComb *et al.* [12] |

Not only was this general interest in faces greater toward conspecific faces than for other species, but the same pattern was demonstrated for conspecific skulls, and to a lesser extent for “conspecific” stones, indicating that the main factor driving their interest was faces, in particular conspecific face-like stimuli. Moreover, the conditional models for all three conditions of experiment 1, show significant effects for *species chimp* (all types pooled) when compared to all three other *species* (all types pooled). What this suggests is that chimpanzees can extract familiar, face-like features from skulls (which retain multiple face-like features) although less so from objects (stones) only resembling faces/skulls in outline. Moreover, compared to frontal/diagonal orientations, the effects were weaker for lateral orientations than for frontal and diagonal orientations across all stimuli, presumably because lateral orientations carry less information about faces.

For experiment 1, in the frontal condition, chimpanzees showed a clear interest in frontally presented conspecific skulls; significant differences in looking times were noted for the chimpanzee skull *versus* all other non-conspecific skulls in this orientation. They also showed a high degree of interest in frontal conspecific faces, with their attention significantly greatest for chimpanzee faces relative to the *dog*, *cat*, and *rat faces*. For the frontally oriented stones, chimpanzees again looked longer at the conspecific-like stones compared with the non-conspecific exemplars, but the looking durations were lower overall and the differences non-significant, except when compared to *dog-shaped stones*. This suggests the stones, showing only the outlines of each species, were a too degraded facial stimulus-type to retain their interest; a trend also shown for stones presented in other orientations.

In the diagonal condition for skulls, while chimpanzees exhibited the longest looking durations toward *chimpanzee skulls* the difference was only significant when compared to *dog skulls*. Looking times were also of relatively long duration for the *cat skulls*, one possible explanation being that the feline skull has neotenic features at this orientation (a round skull and large orbits show a passing resemblance to an infant chimpanzee or monkey skull), and future research could address this. For diagonally-presented faces, chimpanzees again showed a clear interest – significant differences in looking duration were noted for the chimpanzee face *versus* all three non-conspecific face-types. These looking times for faces were also slightly higher in comparison to skulls. For diagonal stones, looking durations were yet lower overall, and lowest for the *chimpanzee-shaped stones*, suggesting the stimuli lost much of their semblance to a chimpanzee face at this orientation. No significant effects were found, except for *cat-shaped stones* (longer) compared to *chimpanzee-shaped stones* (shorter).

In the lateral condition, fixations were decreased overall in comparison to diagonal and frontal conditions and there were no significant differences among stimuli, (except for *chimpanzee faces* compared to *cat* and *rat* faces) supporting the general idea that lateral orientations carry the least amount of facial/face-like information. The means were higher for chimpanzee stimuli across all types, however, no significant interaction was found between species and type except for the face sub-condition. As previously mentioned, the conditional models did yield significant results for species alone: the pooled stimuli (skull+face+stone) revealed that chimpanzees looked significantly longer at laterally-presented chimpanzee stimuli compared to other species stimuli in the same orientation, the same was true for frontal and diagonal orientations. One puzzling aspect of the lateral skull presentation was that chimpanzees seemingly attended more to the rat skull than to any other skull. I suspect this was due to the superficially open-mouth appearance (as if vocalising); lateral orientations of rodent skulls make their diastema (space between front-facing teeth and remaining teeth) prominently visible. A lower-level explanation is that the diastema makes the rat skull look perceptually salient causing it to stand out from all the other three. In an additional test, when I covered this area with bone texture, the chimpanzees no longer looked longer at the rat skulls relative to other non-conspecific species, but neither did the differences in their looking times reach significance for any other skull.

In experiment 2, chimpanzees were presented with *chimpanzee faces* together with *chimpanzee skulls* and *chimpanzee-shaped stones*, in frontal, diagonal, and lateral orientations. The combined results show that chimpanzees looked overall longer at *chimpanzee faces* followed by *chimpanzee skulls* and then *chimpanzee-shaped stones*. While the results were significant for *chimpanzee faces* compared to *skulls* and *stones*, the latter two when compared with each other were not significant, although these were close to significance suggesting that a larger sample size might reveal these differences to also be significant.

In Experiment 3. the specific areas within the *chimpanzee skulls* at both frontal and diagonal orientations, chimpanzees looked longer at the teeth, followed by the nasal area, and least toward the eye regions. The looking patterns were significantly longer for both teeth *versus* eye sockets, and also for teeth *versus* nose cavities. These findings support both McComb's study, in which elephants exhibited a greater interest in elephant tusks, and Watts' prediction that chimpanzee skulls may represent iconic features of chimpanzee faces, notably in having teeth (McComb et al., 2006; Watts, 2020).

In conclusion, the most parsimonious explanation for these results is that chimpanzee skulls, essentially, exhibit a degraded signal of a face. Albeit impoverished, skulls nevertheless retain face-like features and appear to be subjected to the same facial biases. Presumably the *relational properties* that linger in the skull (facial outline, teeth, nose cavity, eye sockets), activate a domain-specific face detection module that directs chimpanzees' attention to these approximated facial features.

## 4.4. Framing the results within face perception research

As in the present paper, *own-species facial bias* has been extensively documented in the human and non-human primate literature seemingly developing through *perceptual narrowing* (i.e. distinct areas of the brain become attuned to the faces individuals are exposed to most throughout development) (reviewed in Scott & Fava, 2013). While most of these studies employed methodologies different from our own, three are worth mentioning as the simultaneous presentation of competing stimuli mirror ours. Research in humans using preferential looking found that while neonates did show a preference for human faces over non-human primate faces, they did not make such a distinction when whole bodies were presented. In contrast, 3.5- and 6-month-olds showed a preference for human faces and human bodies when these were presented alongside non-human primates (rhesus monkeys or gorillas) (Heron-Delaney et al., 2011). These findings were reproduced in a similar study in which human and monkey faces were used; 3-month-olds showed a clear preference for human faces, particularly the eyes (Di Giorgio et al., 2012). Lastly, a preferential looking study involving rhesus monkey subjects found that 3-week-old individuals were already better at locating face stimuli over non-face stimuli, and by 3 months of age, they attended to conspecific faces over non-conspecific faces (Simpson et al., 2017).

Our research also builds upon previous findings using eye-tracking. Kano and Tomonaga (2009), using naturalistic images of humans, chimpanzees, and non-primate mammals, found that both humans and chimpanzees fixated first on faces, but that chimpanzees shifted their gaze more quickly. Similar results were found with gorillas and orangutans (Kano & Tomonaga, 2012). Furthermore, chimpanzees tended to fixate longer towards eyes, mouth, and nose respectively (Kano & Tomonaga, 2010) while bonobos tended to look more at the eyes compared with chimpanzees, though both species look longer overall towards the eyes *versus* the mouth (Kano et al., 2015). Strikingly, Hirata and colleagues (2010) showed that although chimpanzees look more at the eye region of conspecific faces, when the eyes were closed they looked longer at the nose region followed closely by the mouth. This was mirrored, to some extent, in our study, given that the eye region of skulls (not having eyes) received lesser attention compared to teeth.

Much like our findings, other experiments also suggest processing differences between facial stimuli presented frontally and in profile. In a visual search task using touchscreens, Tomonaga and Imura (2015) found that while chimpanzees were efficient at searching for forward-facing faces (human and chimpanzee), they were significantly slower at detecting faces shown in profile. This is echoed by previous facial recognition research on humans which consistently found poorer performance (slower reaction + lower accuracy) in trials using faces in profile compared to frontally-facing (Bruce et al., 1987; Hill et al., 1997; Rose et al., 2002). One face detection study using visual search in natural scenes found that participants' performance was equally good for frontal and diagonally presented faces, but declined for faces in profile, this effect persisted even when only the upper halves of faces (eyes+nose bridge) were visible, but not for the lower portion (nostrils+mouth) (Burton & Bindemann, 2009). Similar findings were also confirmed by Bindemann & Lewis (2013). Moreover, an eye-tracking study revealed that when human faces were viewed in profile, the perceived intensity of the facial expression was reduced compared to frontal and diagonal conditions (Guo & Shaw, 2015). Presumably, this is connected with direct gaze. According to Senju and Hasegawa (2005), a direct gaze signals the valence of intention towards the receiver (i.e. communicative, affective, hostile, friendly, or sexual) making it adaptative to direct attention towards front-on faces. This ability follows a developmental trajectory that starts with front-on faces being processed in dedicated areas of the brain, and somewhere around 8 months of life, side-on faces are integrated into the same brain regions (Nakato et al., 2009). This is perhaps unsurprising since faces and bodies in profile are also involved in more elaborated computations such as decoding social cues (intentions/actions) towards third parties or objects (*sensu* Hattori et al., 2010).

Neuroimaging research in humans has shown three distinct regions in the brain to activate when facial stimuli are presented. Within this dedicated network for face selectivity, the *fusiform gyrus* is considered its most robust and selective component (Saygin et al., 2012), followed by the *superior temporal sulcus* and the *lateral occipital cortex* (Parr, 2011). In comparison, macaques (*Macaca mulatta*), while lacking a clear hemispheric specialisation and a *fusiform gyrus*, do show face selectivity in the *superior temporal sulcus* (Tsao et al., 2008) and the *inferotemporal cortex* (Arcaro et al., 2020). However, research in vervets (*Chlorocebus aethiops*) identifies a hemispheric asymmetry in favor of a stronger neuronal activation in the right *inferotemporal cortex* (Zangehnepour & Chaudhuri, 2005). Furthermore, marmosets (*Callithrix jacchus*) show activation in the *superior temporal sulcus* as well as the *occipital cortex* (Hung et al., 2015). In chimpanzees, face perception is not visibly lateralised as in humans, but activation of the *fusiform gyrus* as well as the *superior temporal sulcus* and the *orbitofrontal cortex* to face stimuli supports the claim that their facial processing is similar to humans (Parr et al., 2009). Taken together, these studies raise the possibility that, while the *fusiform gyrus* specialization emerged recently in evolution and developed in humans and other apes, there is still a deep homology for face selectivity in specific brain areas of both Old World and New World primates.

Our findings are also in line with research in *face pareidolia* (detection of illusory faces on non-living objects) carried out in humans (Liu et al., 2014), chimpanzees (Tomonaga, 2013), and rhesus monkeys (Taubert et al, 2017) where inanimate face-like artifacts are perceived as faces. Neuroimaging analyses in humans situate illusory faces in the *fusiform gyrus* (specifically the *right fusiform face area*) (Luo et al., 2014; Akdeniz et al., 2018) and indicate that, over time, this initial face detection migrates into brain areas dedicated towards object processing, suggesting recategorization from animate to inanimate (Wardle et al., 2020). The chimpanzee skull, I argue, falls within this class of highly pareidolic objects.

Thus, whereas the relationship between the face and the skull is not incidental (skulls functionally support faces and protect the brain), the attention towards forward-facing skulls is.

This attention towards chimpanzee skulls is best explained as the by-product of a facial module (i.e. a network of specialized brain regions) originally evolved for processing facial features and emotional expressions.

## 4.5. Ecological considerations

There are some considerations regarding chimpanzee/elephant ecologies. First, most chimpanzees live in rainforest environments not conducive to the long-term preservation of bones. Woodland-savannah sites (i.e. Fongoli, Senegal, or Issa Valley, Tanzania) might be better candidates for observing chimpanzee-skeleton interactions. But living in rainforests should not impact shorter-term interactions. Forest elephants do live in these environments and have been known to interact with the carcasses and bones of conspecifics. Two recent papers describe such visitations using camera traps; Stephan et al. (2020) recorded 193 visits over 8 months, and Hawley et al. (2017) recorded 5 visits for 3 months. Chimpanzee remains, however, are typically collected for later pathological/anatomical/biomedical analysis (at some field sites though not all) (Pettitt & Anderson, 2020), eliminating any potential interactions chimpanzees might have with them and therefore likely accounting for the paucity of observations (Watts, 2020). For instance, a taphonomic study in Kibale recovered the remains of nine chimpanzees including the skulls (five complete with jawbones), while the remaining skeletal parts (ribs, fore, and hind limbs) were either entirely missing or incomplete (Peterhans et al., 1990). Dying on the forest floor might further accelerate scavenging, Yamagiwa (1998) found the partially complete skeleton of an adult male chimpanzee in a one-month-old tree nest with other newer nests in the vicinity.

Second, unlike reported behaviour in elephants, chimpanzees show curiosity to all sorts of similar-sized dead animal species (i.e. aardvark, bushpig, bushbuck, leopard, monkeys) (Anderson, 2018; Gonçalves & Carvalho, 2019). Chimpanzees are likely aware of conspecific skeletons in their environments and these encounters are severely underreported. This knowledge also extends to situations where mothers carry dead infants to the point of mummification/skeletonization (Biro et al., 2010). Prey-species with similar anatomy such as monkeys are also potentially informative; Boesch and Boesch (1990) report on a juvenile chimpanzee with a colobus monkey skull using a tool to scoop out the brain, and another case involved an adult female using sticks to clean the eye-sockets of a colobus skull after she had finished eating the eyes. Moreover, in some parts of Africa, chimpanzees are sympatric with lowland gorillas (for lethal encounters, see Southern et al., 2021), and gorilla skeletons, exceedingly similar to chimpanzees, are likely encountered. Naturally, being the largest extant land mammal, on dying, elephants leave the largest skulls in their habitats (roughly twice as large as a hippopotamus or a rhinoceros), the only other skulls that bear a superficial resemblance to theirs are those of their closest living relatives, the sirenians (dugongs and manatees) which, being strictly aquatic species, do not share the same habitats.

Finally, elephant tusks and chimpanzee teeth are tied to different contexts. Chimpanzee skulls bear a resemblance to particular facial expressions such as the fear grin and pout face. Likewise, chimpanzees' teeth become visible during screams, and also during yawning or feeding. On the other hand, elephant tusks, always visible, can assume a more neutral character. Furthermore, without trunks and ears (two critical elements for communication) elephant skulls little resemble an actual elephant face. There remains the issue of whether chimpanzees in the wild associate skeletons with the places where dead individuals were previously seen. Just as with McComb et al.'s study, our experiment demonstrates a general propensity in chimpanzees to look at same-species skulls which appears to be based perceptually, but this does not address directly whether they categorize skeletons or skulls as part of a dead conspecific, a question which would benefit from further exploration. Regarding to what extent and how chimpanzees might behave towards skeletons in the wild, in light of our findings, two, not necessarily mutually exclusive, explanations can be advanced: chimpanzees pay attention to conspecific chimpanzee skeletons (particularly to the skull as a byproduct of face-processing skills), and they may infer this meaning (and in some cases the identity of the individual) from the places in which they are found. Such questions may also have a bearing on research into the *landscapes of fear and disgust*, investigating whether dead bodies provide information on danger due to predation or pathogens (*sensu* Moleon & Sanchez-Zapata, 2021).

## 5. Conclusion & Future Directions

I began this study with the central assumption that chimpanzee skulls are perceived like degraded chimpanzee faces and that they would likewise be subjected to the same biases. I proposed three working hypotheses: H1a, chimpanzees look longer at conspecific stimuli *versus* non-conspecific stimuli (conspecific stimuli > non-conspecific stimuli); H1b, chimpanzees look longer at frontal/diagonal conspecific stimuli *versus* laterally presented conspecific stimuli (frontal ≈ diagonal > lateral); H2, within conspecific stimuli, chimpanzees look longer at *chimpanzee faces* followed by *skulls* and *stones* (face > skull > stone); and H3, just as elephants direct their attention towards elephant tusks, likewise chimpanzees look longer at conspecific teeth *versus* other facial regions (teeth > eye ≈ nose). Overall, I found support for all three hypotheses. For H1a, chimpanzees exhibited significantly longer looking durations towards conspecific relative to non-conspecific stimuli when types were pooled (see Supplementary Data). They also looked significantly longer across most types (skull and face) and orientations (frontal and diagonal) except for stone stimuli (looking durations were relatively longer toward frontal *chimpanzee stones* but the difference was only significant when compared for dog stones) reinforcing the "degraded face assumption". For H1b, chimpanzees showed significantly longer looking durations for frontal/diagonal conspecific stimuli in comparison to laterally presented conspecific stimuli, again showing similar biases to previous facial research experiments. For H2, with the chimpanzee-only stimuli, the chimpanzees did look significantly longer at the *chimpanzee faces* compared to *chimpanzee skulls* and *chimpanzee-shaped stones*, but this dropped below significance when comparing the *chimpanzee skull* with the *chimpanzee-shaped stone*, although the direction of difference fitted our prediction further supporting the "degraded face assumption". For H3, in the chimpanzee skull regions, our prediction that chimpanzees would look predominantly at the teeth compared to other areas was also upheld. They looked significantly longer at the teeth *versus* the eye socket and the nasal regions of the skull.

The combined results show support for our hypotheses and do suggest a connection between a domain-specific module in the chimpanzee brain directing their attention towards face-like stimuli. This face module evolved and develops within the context of face-to-face interactions (the likely reason all frontal conditions in our experiment, the chimpanzee stimuli received longer-looking patterns overall). The skull contains relevant, albeit impoverished face-like features. This relationship is, of course, not incidental as skulls support faces, but the attention towards skulls appears to be best explained as a by-product of a module originally evolved for decoding facial expressions. Perhaps notably, unlike wild chimpanzees, our captive subjects never interacted with conspecific skeletons. This suggests that, apart from learned associations, similar interest exhibited by their wild counterparts towards conspecific skulls might also be explained by the same recognition mechanism. To further decode the phylogeny of this face-skull relationship, future studies could compare naïve human infants' performance in a similar task (1-3 year-olds familiar with human faces, but with no experience of human skulls). Another research avenue would be to replicate McComb and colleagues' experiment in the laboratory with the aid of a 3D printer (skulls controlled for size and color). Finally, neuroimaging studies could further address the precise connection between skull and face stimuli in the brain.

# Chapter 7. Chimpanzees' attention toward audio/visual death-stimuli

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## 1.1 Introduction: Animacy detection, threat or benefit

Primates and, undeniably other animals, divide their world into agents and non-agents. This *animate-inanimate distinction* runs in parallel to a *living vs non-living distinction*. Animates are classified as living creatures (animals). The following major differences between animate and inanimate entities were highlighted by Gelman and Spelke (1981): 1) animates can act, however, inanimates can only move when something or someone causes them to; 2) animates grow and reproduce; 3) animates can know, sense, emote, learn, and "reason"; and 4) animates are made of biological structures that support life and allow reproduction. Animates usually have clear morphological/biomechanical features that are typically associated with animacy (e.g., eyes, faces, limbs, and biological motion) used to categorize them as such. Piaget was among the first to explore animism as the foundation of children's biological thinking, claiming that they regarded non-living objects as intentional living entities (Piaget, 1929). Contrary to his claims, subsequent research has shown that biological knowledge arises at earlier stages of cognitive development as part of a specific biological domain from which those intuitions are formed (Inagaki & Hatano, 2006; Carey, 2009; Opfer & Gelman, 2011). In general, animate entities, are more effective at capturing attention than inanimate objects, so the existence of distinct brain areas dedicated to processing information on animacy and non-animacy in humans (Caramazza & Shelton, 1998; Gobbini et al., 2011; Sha et al., 2015), but also in non-human primates (Kriegeskorte et al., 2008; Kiani et al., 2009) is perhaps unsurprising.

According to the *animate monitoring hypothesis*, animate entities attract attention due to their role as predators or prey in prehistoric hunter-gatherer cultures (New, Cosmides, & Tooby, 2007). New and colleagues discovered that participants noticed changes to animals (including people) more rapidly and accurately than changes to inanimate things using a *change detection task*. In *visual search tasks*, animate objects are detected faster than inanimate objects (Jackson & Calvillo, 2013), are looked at longer than inanimate objects (Yang et al., 2012), and are better remembered than inanimate objects (Bonin, Gelin, & Bugaiska, 2014), and are detected more frequently in an *inattentional blindness task* (Calvillo & Jackson, 2014). The term inattentional blindness refers to the failure to notice unexpected objects/entities during visual scenes while engaging in an attention-demanding task. A famous example is "the invisible gorilla experiment" by Simons and Chabris (1999) where participants tracking a basketball in a movie failed to perceive the appearance of a human dressed in a gorilla costume. For example, snakes have long been known to prey on primates, the primate visual system and fear reaction may have evolved to identify and respond to snake threats (Öhman & Mineka, 2003; Isbell, 2006). The *snake detection effect* whereupon snakes are detected more quickly has been supported by research in human children (Lobue & DeLoache, 2008) and adults (Öhman et al., 2001; Soares et al., 2009; Soares & Esteves, 2013), and also and nonhuman primates (Shibasaki & Kawai, 2009; Zhang et al., 2020) detect snakes more quickly than other items, according to several studies. Supporting the *animate monitoring hypothesis*, a recent study (Calvillo & Hawkins, 2016) found that rather than threatening objects (guns) or dangerous animals (snakes), humans generally attend to animate entities than inanimate objects with no significant difference between snakes or other animate beings (birds).

## 1.2. Experimental framework: The animacy bias

The detection speed of standing lions and impala in natural situations was measured using eye-tracking on humans. Lions had stronger attention-grabbing properties (Yorzinski et al., 2014). Furthermore, standing lion targets were presented with lion distractors, and standing impala targets were presented with impala distractors that were either facing towards or away. Both facing lion and impala targets were detected faster than when they were facing away while facing lions had a faster detection latency than facing impalas (Yorzinski, Tovar, & Coss, 2018). Because lions' standing posture could be a key indicator of their dangerousness, researchers compared standing lions to reclining lions and standing impalas to reclining impalas. Contrary to their expectations, they found that regardless of species, both lions and impalas in standing postures were detected faster than reclining ones (Yorzinski & Coss, 2020).

The experiment led by Yorzinski & Coss (2020) yielded some curious results. While their conclusions are strictly within a predator-prey explanatory framework, their results are in line with the *animate-monitoring hypothesis*. Those findings can be distilled into a simple perceptual rule: “if the animal is standing, attend to it”, since they represent a more immediate prompt. In real-life scenarios, an upright live animal in immediate proximity will either run towards (predator) or run away from (prey) the observer. So it stands to reason that such attentional predisposition would be widespread across many non-human animals as well.

Since dead animals are an inexorable entity in nature, while not having *dynamic cues to animacy* but still displaying *static cues to animacy* (Gonçalves & Biro, 2018), it raises the question that if a live animal is shown together with a dead animal, such *animacy bias* as shown by differential looking patterns would also be in place using similar methodologies. The visual aspects of death cues can be divided into three major categories: *serious injuries*, *inertia*, and *decomposition*. While *serious injuries* and *decomposition* are easily depicted in images and arguably better diagnostics of the state of death, *inertia* merely translates into the body being exhibited in prone or supine positions on the ground which can be confused with sleeping, thus no fresh bodies would be used but showing either two of these cues (inertia+decomposition, or inertia+grievous injuries). Moreover, chimpanzees are known to make all sorts of vocalizations surrounding death from low emotional intensity (“huu” calls, whimpering) to higher emotional intensity (alarm calls, screams). However, using dynamic stimuli (videos) of chimpanzees' interactions with dead conspecifics (dead infant carrying, physical interactions with dead adults) inertia in the corpse is more salient as it stands in contrast with live moving conspecifics.

The question of whether chimpanzees (and other animals) have a concept of death is a thought-provoking, albeit problematic question to tackle methodologically. One avenue to explore this issue started with the question: how do chimpanzees perceive death-related states in comparison to life-states? If they have differential looking patterns when dead and live animals are shown on a screen (i.e. animacy bias). Or if chimpanzees perceive death as something bad, or associate negative emotional calls with odd states (i.e. an inanimate conspecific). To explore this I devised two experiments: for the first one I presented the chimpanzees with images of live and dead animals in realistic backgrounds and for the second experiment I presented two simultaneous 10-second videos depicting live and dead chimpanzees together with chimpanzee vocalizations (either positive, negative, or neutral).

## 2. Materials and Methods

### 2.1 Subjects

The experiment initially included eight adult chimpanzees (*Pan troglodytes*), three males and five females. All individuals were housed at the Primate Research Institute, Kyoto University, Japan. These individuals were members of two social groups (totaling 11) living in an environmentally enriched facility comprising two outdoor enclosures (250 $m^2$ and 280 $m^2$), an open-air outdoor enclosure with vegetation and climbing structures (700 $m^2$), and indoor living rooms linked to the testing rooms (Ochiai & Matsuzawa, 1999). They had access to water *ad libitum* and received a variety of foods several times a day. All research procedures followed institutional guidelines (Primate Research Institute 2010 version of 'The Guidelines for the Care and Use of Laboratory Primates') and the experimental protocol was approved by the Animal Welfare and Animal Care Committee of the Primate Research Institute and the Animal Research Committee of Kyoto University.

### 2.2 Apparatus

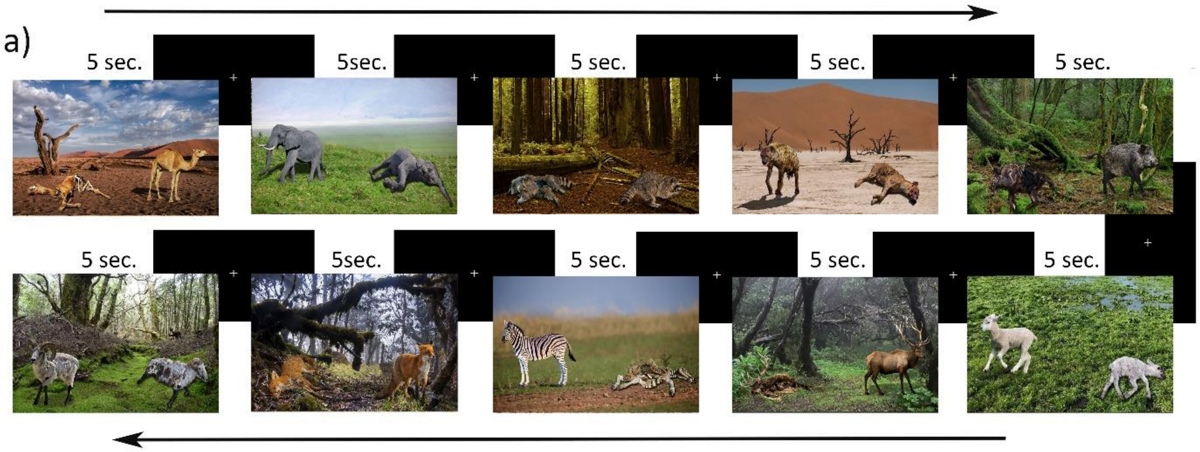
This research was conducted in an experimental booth (1.80 × 2.15 × 1.75 m) inside a testing room. Each chimpanzee voluntarily walked to the booth through an overhead walkway connected to the indoor rooms and outdoor enclosures. I used a Tobii eye tracker (60 Hz; X300; Tobii Technology AB, Stockholm, Sweden). Sets of images were shown at a resolution of 1280x720 pixels on a 23-inch LCD monitor (ca. 43x24 degree) using TobiiStudio software (v. 3.2.1.) at approx. 60 cm. Both the eye-tracking device and the monitor were outside the experimental booth, the subject's eye movements being recorded through a transparent acrylic panel (1 cm thick). To reduce head movements during stimulus presentation, the subjects were able to sip juice through a nozzle and tube attached through a hole in the acrylic panel (see the previous Chapter). At the beginning of each test session, automated calibrations were conducted for each subject, these involved one small clip of a stirring object presented twice on each opposing corner of the screen. Following these measures, calibration errors were typically within one degree (Kano & Tomonaga, 2011).

### 2.3 Procedure and Stimuli

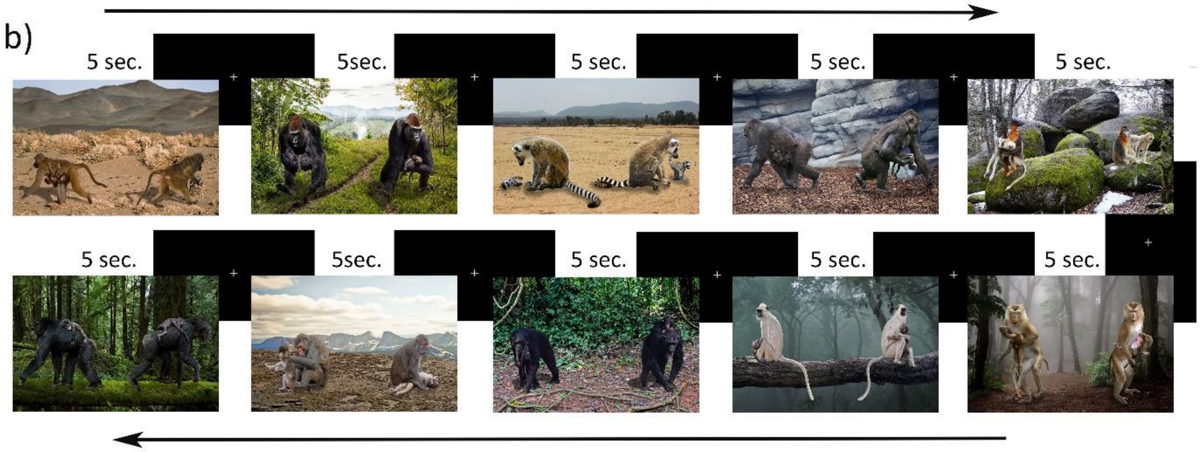
Experiment 1, comprised of two conditions: 1) dead-live animal condition and 2) dead-live infant primate condition. For condition 1, I presented a total of 20 images to the chimpanzees. Each image comprised two animals of the same species, all were terrestrial mammals (i.e. boar, deer, fox, hyena, etc) placed on the far left and far right sides of the screen both placed in a realistic background (forest, desert, prairie, meadow, etc). In each image, the animals were represented in two states: dead and alive at matched orientations as possible. No image pairs nor backgrounds were repeated and the order was counterbalanced. Each image group was presented for five seconds and both first times to fixation and looking durations were measured. All live animals were depicted standing with neutral bodily expressions while all the dead animals were lying down in the initial to active stages of decomposition (but not advanced decay or skeletonized stages) with disruptions of the body envelope. To control for potential communicative gaze or head direction, both animals were always facing away from each other. For condition 2, I also presented a total of 20 images. Each image comprised of two primate adult females of a particular species (chimpanzee, macaque, langur, gorilla, baboon, etc) engaging in infant carrying placed on the far left and far right sides of the screen both placed in realistic backgrounds just as in the previous condition. In each image only the infants were represented in two states: dead and alive, both their and their mother’s position were matched with each other as much as possible. Due to the scarcity of dead infants carrying pictures in non-human primates (condition 2) compared to other terrestrial mammals (condition 1), the dead infants were shown in several stages of decomposition (fresh to mummified). Each image-group was presented for 5 seconds and was followed by a fixation cross at the middle. On each stimulus image (i.e. live and dead animal) I drew areas of interest (AOIs) slightly larger (10-15%) than the original stimuli to account for possible fixation errors. The AOIs were the same size for each of the corresponding dead and live animal pairs.

For experiment 2, I presented two simultaneous videos on each side of the screen. All videos depicted chimpanzee only-stimuli (mostly mother-infant interactions). In one video the infant was alive, while on the other it was dead. All video pairs were presented within a 10-second window of time (10 video pairs in total). For the control condition, these videos were presented with white noise. For the two subsequent experimental conditions, the same videos were shown a week apart from the control and paired with negative vocalizations (alarm calls, screams, “huu” calls) and positive vocalizations (grunting, laughter, and grooming sounds: lipsmack/raspberries). These were counterbalanced for the subject (see Figure 7.1 for a clear view of the experimental design).

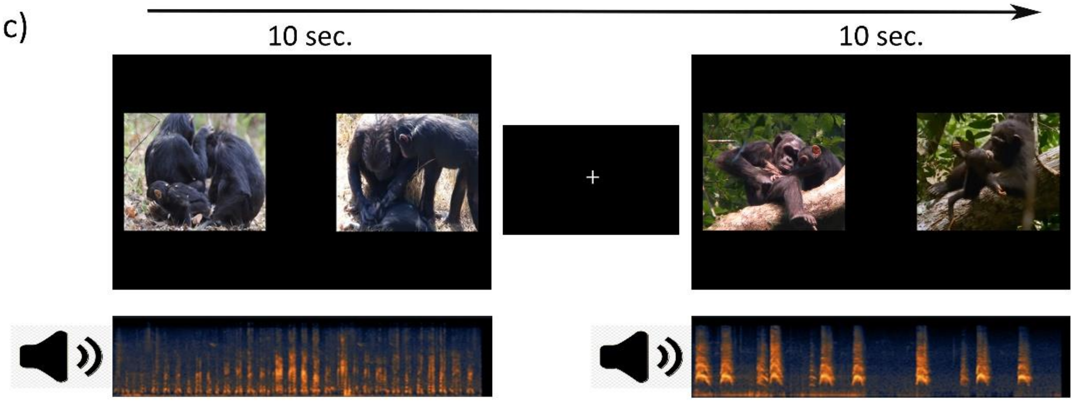
In experiment 1, eye movement data were filtered using a Tobii fixation filter. For looking time methods, I used both the *total fixation duration* and *time to first fixation* measurements generated by the Tobii Studio software. For experiment 2, only *total fixation duration* was measured. Total fixation duration is the sum of the duration of all fixations (in seconds) occurring during stimulus presentation while time to the first fixation indicates the minimum amount of time the first saccade occurred (shorter times indicating faster eye movement towards the area of attention).



Experiment 1 (animal condition) Session 1 (of 2)



Experiment 1 (primate condition) Session 1 (of 2)



Experiment 2 (negative condition) Session 1 (of 5)

Figure 7.1. Experimental design flow for the two experiments.

### 2.4 Statistical Analysis

For the first experiment (dead-live images), in the *live-dead animal condition*, to detect any viewing preferences, I conducted two separate linear mixed models (LMM) for both total fixation duration and *time to first fixation* data. Observations For the analyses, I set “type” (dead, alive) and “species” as within-subject factors, “gaze” (total fixation duration/time to the first fixation) as a dependent variable with “subject” (chimpanzee participants) nested in “trial” as random factors. Similar procedures were done for the *live-dead primate condition* but (due to the similarity of primate body plans) with the factor “species” dropped. For the *time to first fixation*, samples below 200 ms were excluded since spontaneous gaze movement response to stimuli usually occurs after that period (Kano & Tomonaga, 2009).

For the second experiment (dead-live videos), I presented two chimpanzee video pairs, each pair shown simultaneously (dead + alive), for a total of five sessions. Three separate linear mixed models (LMM) were also conducted with all three conditions (control, positive and negative stimuli) with “gaze” as a dependent variable, “type” (dead, alive) as a within-subject factor, and “subject” nested in “trial” as random factors.

All statistical analyses were conducted on the package lme4 with the gaussian family and the identity link function.  Significance for whole model terms was assessed with the “anova” and “drop1” function for experiments 1a and 1b plus 2, respectively. *Post hoc* pairwise Bonferroni-corrected comparisons among levels (species and/or type) were conducted using the *emmeans* package. All analyses were conducted on R 4.1.0. (R Core Team, 2018).

## 3. Results

### 3.1 Experiment 1 (Dead-Live Images)

In the *live-dead animal condition* (condition a), for the total duration of fixations (observations, N=320), there was a significant interaction between “species” and “type” (*F*=1.818, df=19, *p*=0.0208). Additionally, significant main effects were obtained for “type” ( *F*=13.457, df=1, *p*=0.00029) and “species” (*F*=1.824, df=19, *p*=0.0208). These indicate the chimpanzees looked significantly longer at *live animals* ($\bar{x}$ = 1.19 seconds) in comparison to *dead animals* ($\bar{x}$ = 0.89 seconds) and, some species pairs recruited more attention than others. The following *post-hoc* tests showed that despite longer-looking durations in 13 out of 20 image pairs, these were not significant, except for 6 image pairs (boar, goat, hyena, impala, ram, and zebra) of which the chimpanzees did look significantly longer at the live animals. Conversely, no significant longer looking durations for dead animals were observed (see table 3.1).

Table 3.1. Looking durations in the paired sample analysis. Significant results shown in bold.

| species | dead (sec) | alive (sec) | t-ratio | p-value | eff size | CI Lower | CI Upper |
|---|---|---|---|---|---|---|---|
| badger | 0.77 | 0.541 | 0.663 | 0.5079 | 0.332 | -0.65 | 1.31 |
| boar | 0.931 | 1.864 | -2.703 | **0.0073** | -1.351 | -2.34 | -0.36 |
| buffalo | 1.034 | 1.14 | -0.308 | 0.7583 | -0.154 | -2.34 | -0.36 |
| camel | 1.359 | 1.333 | 0.656 | 0.5125 | 0.328 | -0.64 | 1.31 |
| elephant | 1.653 | 1.379 | 0.793 | 0.4282 | 0.397 | -0.58 | 1.38 |
| elk | 0.611 | 1.038 | -1.235 | 0.2177 | -0.618 | -1.6 | 0.36 |
| fox | 0.629 | 0.881 | -0.732 | 0.4649 | -0.366 | -1.35 | 0.61 |
| goat | 0.625 | 1.549 | -2.677 | **0.0079** | -1.339 | -2.32 | -0.34 |
| hippo | 0.746 | 0.595 | 0.438 | 0.6614 | 0.219 | -0.76 | 1.2 |
| horse | 1.026 | 1.2 | -0.504 | 0.615 | -0.252 | -1.23 | 0.73 |
| hyena | 0.814 | 1.593 | -2.257 | **0.0248** | -1.129 | -2.11 | -0.13 |
| impala | 0.696 | 1.384 | -1.993 | **0.0473** | -0.996 | -1.98 | -0.01 |
| lamb | 0.946 | 0.861 | 0.246 | 0.8056 | 0.123 | -0.86 | 1.1 |
| leopard | 1.486 | 1.315 | 0.496 | 0.62 | 0.248 | -0.73 | 1.23 |
| llama | 0.88 | 1.345 | -1.348 | 0.1788 | -0.674 | -1.65 | 0.31 |
| racoon | 1.325 | 0.682 | 1.844 | 0.0663 | 0.932 | -0.06 | 1.92 |
| ram | 0.641 | 1.995 | -3.924 | **0.0001** | -1.962 | -2.95 | -0.96 |
| tapir | 0.72 | 0.885 | -0.478 | 0.6329 | -0.239 | -1.22 | 0.74 |
| wolf | 0.634 | 1.254 | -1.797 | 0.0734 | -0.899 | -1.88 | 0.08 |
| zebra | 0.466 | 1.226 | -2.203 | **0.0284** | -1.101 | -2.09 | -0.11 |

For the time to first fixation (observations, N=292) there was a significant interaction between "species" and "type" (*F*=2.760, df=19, *p*=0.00017). In addition, there was a main effect for both "type" (*F*=17.36, df=1, *p* <.0001), and "species" (*F*=2.377, df=19, *p*= 0.00135). These results show that chimpanzees detected images of *live animals* ($\bar{x}$ = 0.55 seconds) faster than *dead animals* ($\bar{x}$ = 0.92 seconds) and there were particular species they detected faster than others. (see Figures 7.2 & 7.3).

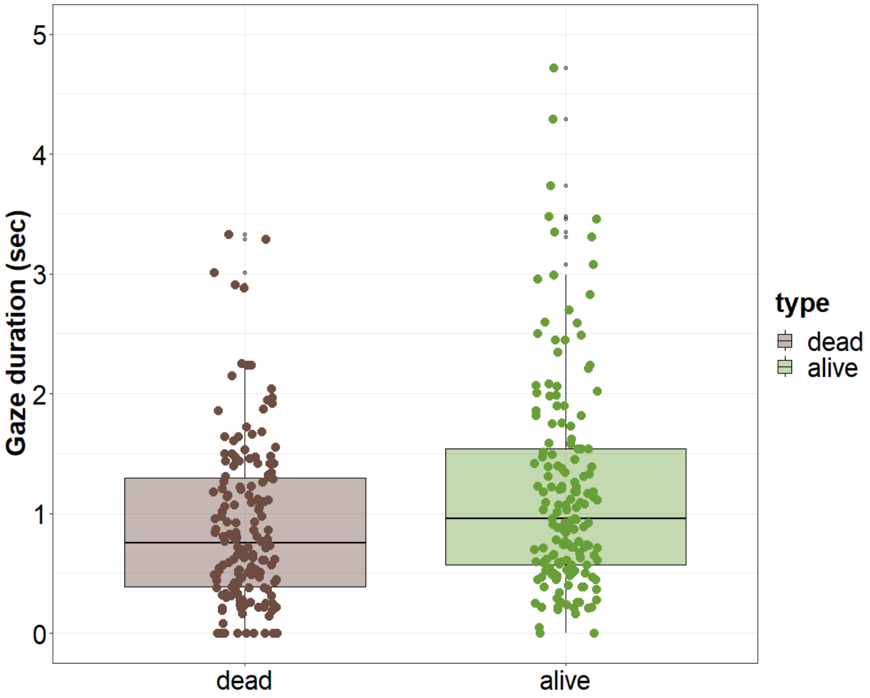


Figure 7.2. Total fixation duration values for the live-dead animal stimuli. Each dot represents a single trial.

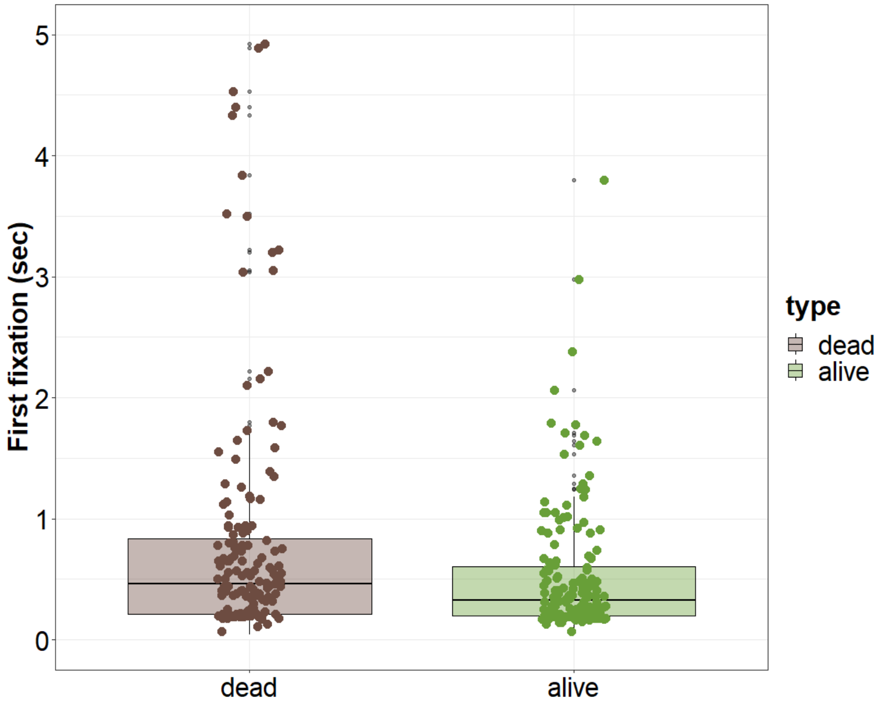


Figure 7.3. Time to first fixation values for the live-dead primate stimuli. Each dot represents a single individual's trial.

In the *live-dead primate condition* (condition b), for the total duration of fixations (observations, N=320), there was a significant result within "type" (live vs dead) (χ2=33.37, df=1, *p*<.0001). The following *post-hoc* tests revealed that the chimpanzees looked longer overall at the *live infant primates* (x̄ = 0.84 seconds) in comparison to *dead infant primates* (x̄ = 0.45 seconds) (t=-5.777, *p*<.0001). For the time to first fixation (observations, N=304) there was no significant result within "type" (live vs dead) (χ2= 0.12, df=1, *p*=0.7224). The following *post-hoc* tests revealed that the chimpanzees looked first overall at the *live infant primates* (x̄ = 0.69 seconds) in comparison to *dead infant primates* (x̄ = 0.71 seconds) (t=0.356, *p*=0.7227). (see Figure 7.4 & 7.5).

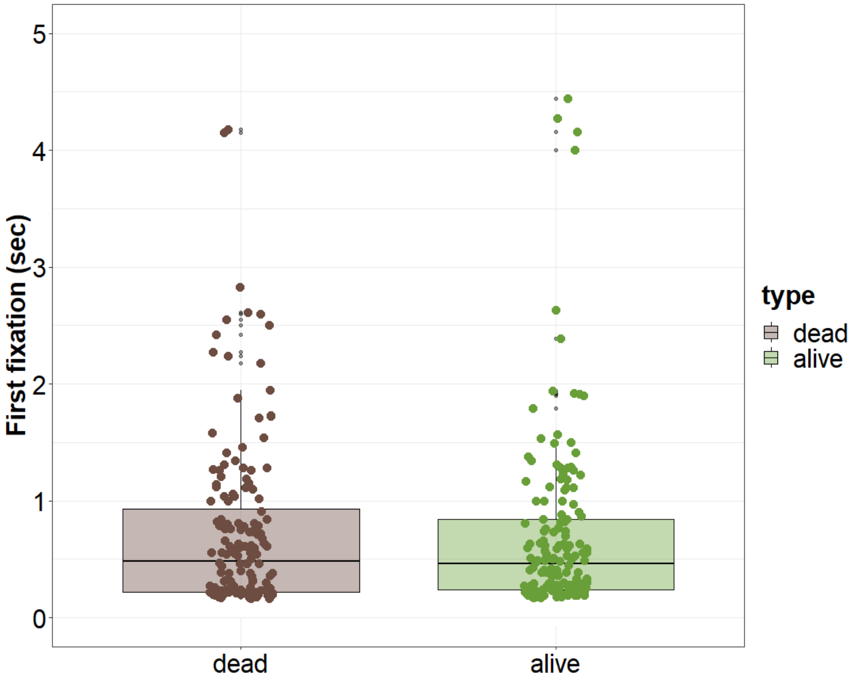


Figure 7.4. Time to first fixation values for the live-dead primate stimuli. Each dot represents a single individual's trial.

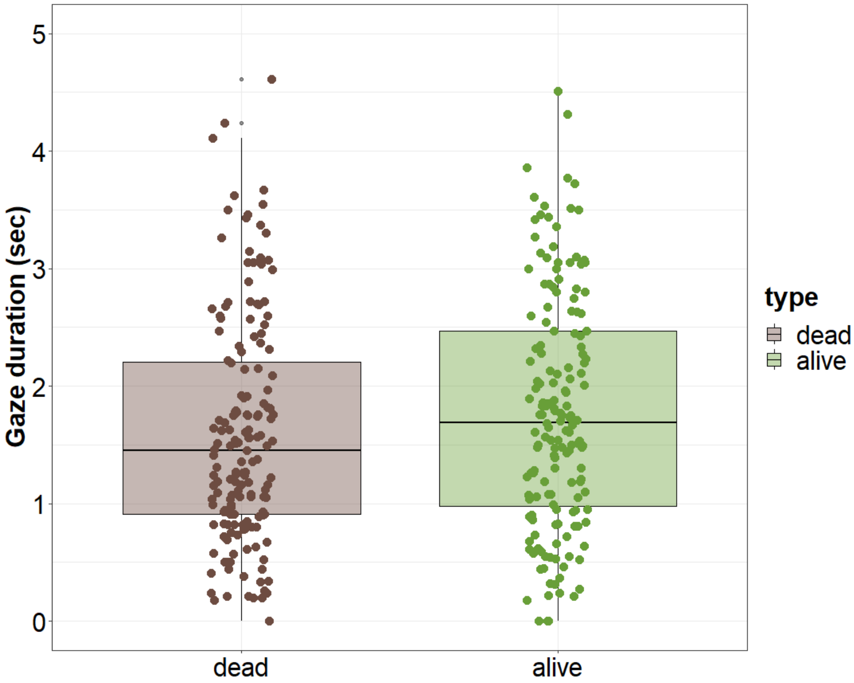


Figure 7.5. Total fixation duration values for the live-dead primate stimuli. Each dot represents a single individual's trial.

### 3.2 Experiment 2 (Dead-Live Videos)

In the *control condition*, for the total duration of fixations (observations, N=64), there was no significant result within type (live vs dead) ($\chi 2$=0.23, df=9, $p$=0.5). Together with a neutral sound, the chimpanzees looked for similar amounts of time to both videos depicting *live chimpanzees* ($\bar{x}$ = 4.48 seconds) and *dead chimpanzees* ($\bar{x}$ = 4.25 seconds). For the *negative condition*, (observations, N=64), again I found no significant results within type ($\chi 2$=0.16, df=9, $p$=0.622). Paired with a negative vocalization, the chimpanzees looked again for similar amounts of time to both videos depicting *live chimpanzees* ($\bar{x}$ = 4.51 seconds) and *dead chimpanzees* ($\bar{x}$ = 4.63 seconds). For the *positive condition* (observations, N=64), I found yet again no significant results within type ($\chi 2$=1.25, df=9, $p$=0.614). Paired with a positive vocalization, the chimpanzees looked again for similar amounts of time to both videos depicting *live chimpanzees* ($\bar{x}$ = 4.37 seconds) and *dead chimpanzees* ($\bar{x}$ = 4.59 seconds). (see Figure 7.6, 7.7 & 7.8).

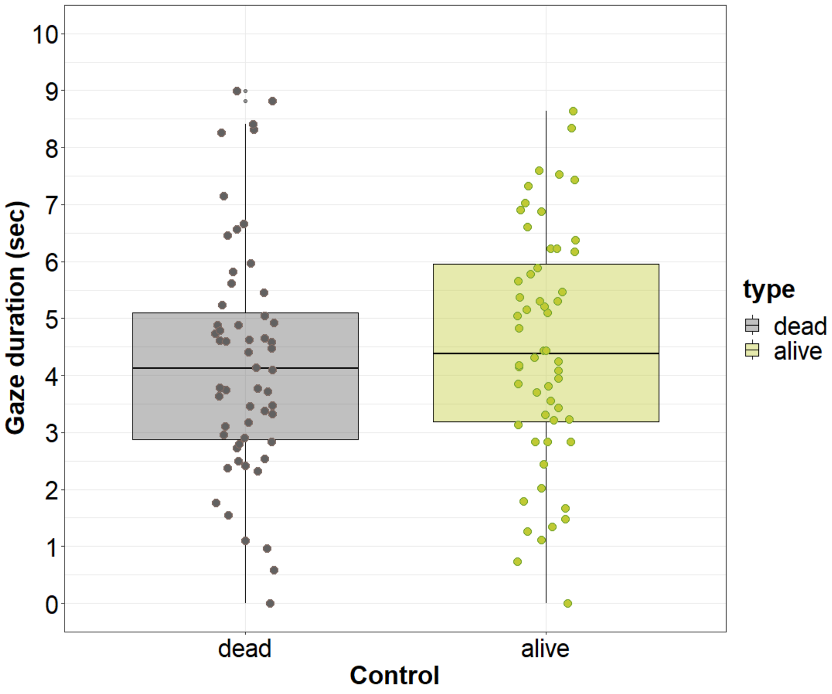


Figure 7.6. Total fixation duration values for the live-dead primate videos (control condition). Each dot represents a single individual's trial.

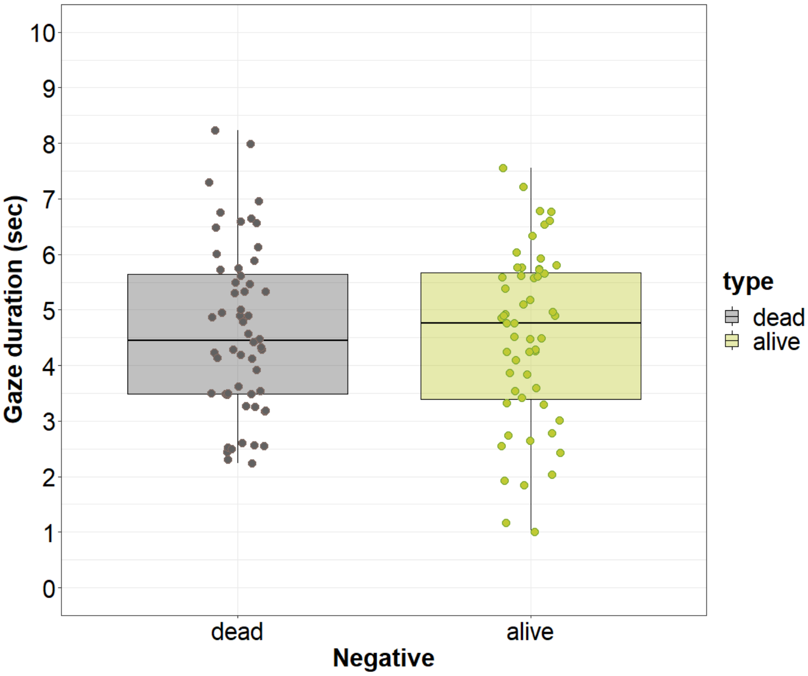


Figure 7.7. Total fixation duration values for the live-dead primate videos (negative condition). Each dot represents a single individual's trial.

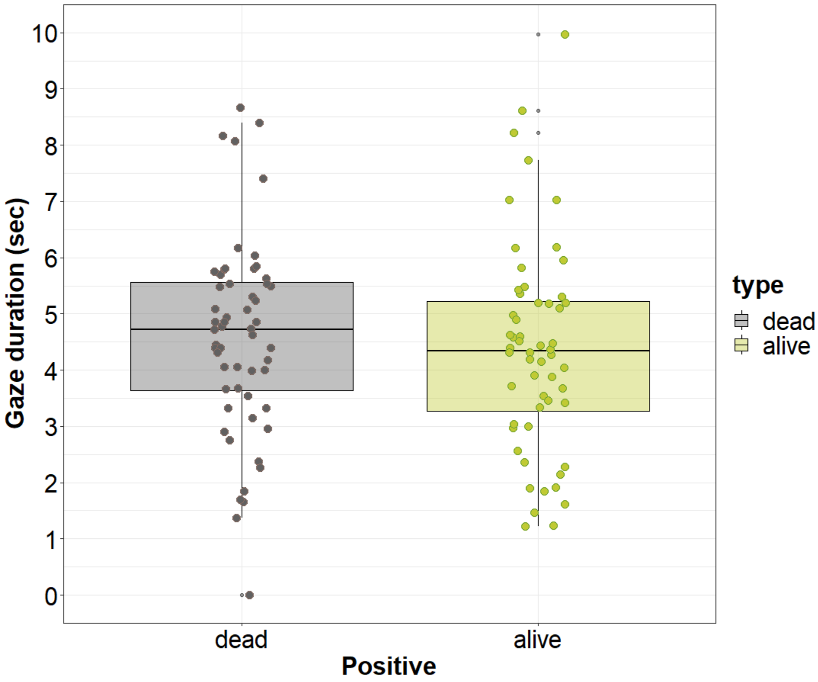


Figure 7.8. Total fixation duration values for the live-dead primate videos (positive condition). Each dot represents a single individual's trial.

# 4. Discussion & Conclusions

Chimpanzees, both in the wild and in captivity, do not live in a vacuum apart from Nature. Throughout their lives, they have plenty of opportunities to interact with other animal species both living and dead as shown by the comparative thanatology literature. While there is a clear advantage from an evolutionary standpoint for animals to detect other agents in the environment (potential prey, predator, or social partner) lesser is known concerning how they perceive dead animals. It is thought that directing attention towards dead conspecifics/non-conspecifics is also evolutionary relevant because corpses might provide information about potential predation events, pathogen hazards, or potential resources.

Since primates' dominant perceptual modality is vision, it was important to define the main visual defining features of death, which include *inertia* (lack of movement), *injury* (severe disruptions of the body envelope), and *decay* (emaciation and putrefaction). To test whether a visual living dead attentional bias exists in chimpanzees, for experiment 1 (condition a), I edited 20 image pairs depicting animal species (terrestrial mammals) both alive and dead in a shared background. Also for this experiment (condition b), I edited 20 more image pairs depicting non-human primate mothers carrying both live and dead infants. The results from condition a) show that chimpanzees look significantly more to images of live animals in comparison to dead animals. Moreover, they detect live “standing” animals faster than dead “prone-supine” animals. This animacy effect whereby subjects detect lifelike animals faster than dead-like animals is consistent with the animate monitoring hypothesis and similar results shown in other eye-tracking studies using humans with living (standing) versus living (lying down) animals whether they be predators (lions) or prey (impalas) (Yorzinski & Coss, 2020). Simply put, the agency system is evolved to monitor potential moving agents faster than resting agents which is then followed by decision-making processes (approach in case of prey, or avoidance in case of predators). Moreover, in my experiment, this animacy effect not only emerged through immediate monitoring, but also carried over to extended monitoring exhibited by longer looking durations at live animals in comparison to dead animals.. In a *post-hoc* analysis that controlled for the variable species in looking durations, I found that the chimpanzees looked longer at the live animals in 13 image pairs out of the 20, but they only looked significantly so at 6 of those 13 pairs. This is not wholly unexpected due to the lowered sample size such analysis entails. Regardless, it still fits the direction of the prediction, worth noting that there were no significant looking durations in the opposite direction (looking more at a dead animal than a live one of the same species). The rationale behind it being that we cannot rule out the possibility that these looking durations were caused by a particular set of features or any specific feature, it would be more appropriate to include it in the analysis. The main argument is that, in general terms, all these live animal images share (more or less) their own same set of cues that are guiding the chimpanzees' attention (standing in life-like positions).

Overall, this *animacy effect* whereby subjects detect faster and/or look longer at lifelike animals than dead-like animals (as shown in both conditions) is consistent with the *animate monitoring hypothesis* and similar results shown in other eye-tracking studies using humans with living (standing) versus living (lying down) animals whether they be predators (lions) or prey (impalas) (Yorzinski & Coss, 2020). Simply put, the agency system is evolved to monitor potential moving agents faster than resting agents which is then followed by decision-making processes (approach in case of prey, or avoidance in case of predators). For condition b) primate-only stimuli, while this *animacy effect* was shown for *extended monitoring* (total looking durations; chimpanzees looked longer at *live infant primates*) this was not the case for *immediate monitoring* (time/latency to the first fixation). One possibility is that the live and dead infants were embedded in two very perceptual similar standing (live) mothers often depicted in the same postures, which, being the larger animates on the screen, would have equally recruited first attention towards them, with the infant targets (live and dead) being secondary to this initial perceptual scrutiny. Moreover, one alternative, though not necessarily mutually exclusive explanation is that live infants carry stronger infantile cues that sustain attention more so than dead infants in several states of decay. Indeed, eye-tracking research has shown that chimpanzees will significantly look longer at live primate infants when they are paired with their mothers (Kawaguchi et al., 2019).

In another line of research, chimpanzees have been seen making a variety of vocalizations in the aftermath of a death, ranging from low emotional intensity (huu calls, whimpering) to high emotional intensity (alarm calls, screams). By employing dynamic cues (videos) of chimps interacting with dead conspecifics (dead infant carrying, physical contact with dead adults), inertia in the corpse becomes more apparent since it contrasts with living moving conspecifics. The rationale behind this experiment was to uncover whether chimpanzees automatically like negative emotional calls to unusual situations (such as inanimate conspecific), and likewise, do they behave more congruently by looking at live conspecifics when positive emotional vocalizations are played back? Surprisingly, my preliminary results show that they do not. It

In conclusion, my findings show that chimpanzees display; 1) significant interest in images of live animals vs dead animals, 2) quicker detection of images of live animals vs dead animals and 3) significant interest in images of live infants vs dead infant primates. The reason for this animacy effect may lie in the *animate monitoring hypothesis*: Live animals pose a more immediate threat and natural selection would have favored this built-in “quicker detection” and increased attention whereas dead animals may be salient in the environment, but lacking agency, they do not require such an active tracking. Future studies could further disentangle where corpses stand in this putative *animacy continuum* where one could explore how inanimate objects capture attention together with dead animals, or likewise, if sleeping animals are placed with dead animals what sort of effect one might expect (i.e. similar *immediate monitoring* for both but more *prolonged monitoring* for the sleeping animal). My second experiment raises more questions than it purports to answer. The reasons behind my results may lie in methodological limitations or individual differences. One possibility is that there might be processing differences between higher vs lower intensity vocalizations negative or otherwise. Another is that chimpanzees being parochial, simply do not care for nor will understand the fate of a chimpanzee outside their group. Finally, it may be that experience matters in this case, and captive chimpanzees populations will differ in the number of experiences they will have with dead conspecifics, while in some facilities it is common practice to allow the animals to interact with their dead, this may not be the established norm.

# Chapter 8. General Discussion and Conclusions

Chapter 1 & 2 - The field of evolutionary comparative thanatology is still relatively new, only now is it at a stage of empirically driven data gathering and hypothesis testing. As a scientific field, it places a strong emphasis on observation, explanation, and prediction of phenomena by producing a body of empirical, theoretical, and practical knowledge concerning the natural world. In contrast, science historiography frequently uses both intellectual history and social history historical methods. Comparative thanatology has had a long and scattered history even before it was named as a specific field. Interest in how non-human animals respond to death can be found in pre-ethological accounts spanning at least two millennia. In chapter 2, I gather for the first time, many of these such accounts, some of which of species that have since become extinct. In them there is a common picture emerges: bonded animals are not wholly indifferent to their dead, quite the contrary. Often they will become distressed, station around and try to produce a response from the dead mate, kin, or group member. More often than not, these animals were humanized and made the subject of pity and compassion. As such, these accounts also give us a glimpse not only into the mental processes of its non-human animals but also of the people recounting them and their own culturally bound ways of thinking about this subject. Outlining the history of this field will hopefully enable future researchers to build upon previously existing knowledge, pursue and refine their research questions and prevent the taking of futile steps (*sensu* Gonçalves & Biro, 2018; Gonçalves & Carvalho, 2019).

Chapter 3 - Evolutionary comparative thanatology benefits from broad taxonomic comparisons of non-human animals' responses to death (Anderson et al., 2018). Furthermore, exploring the sensory and cognitive bases of these responses promises to allow the classification of the underlying mechanisms on a spectrum from phylogenetically ancient to more derived traits. I draw on studies of perception and cognition in invertebrate (Yao et al., 2009; Sun & Zhou, 2013) and vertebrate taxa (Reggente et al., 2016; Anderson, 2016; Swift & Marzluff, 2015), with a focus on arthropods, corvids, proboscids, cetaceans, and primates, to explore the cues that these animals use to detect life and death in others and discuss proximate and ultimate drivers behind their capacities to do so. Parallels in thanatological behavior exhibited by the last four taxa suggest similar sensory–cognitive processing rules for dealing with corpses, the evolution of which may have been driven by complex social environments. Uniting these responses is a phenomenon my colleagues and I term *animacy detection malfunction*, whereupon the corpse, having both animate and inanimate attributes, creates states of fear/curiosity manifested as approach/avoidance behaviors in the individuals interacting with them. I suggest that integrating diverse lines of evidence, including the *uncanny valley effect* (Mori, 1975) provides a promising way to advance the field, and conclude by proposing avenues for future research. This review has brought together observations of living individuals' responses to dead conspecifics in invertebrates and vertebrates, evidence regarding the sensory bases of detecting life and death in others, and potential cognitive underpinnings for animal awareness of death. Together with my co-authors, I have suggested that phylogenetically ancient responses relating to death that are present in many animals exist not only for specific predator detection but also form part of a generalized threat detection mechanism. Presumably in corvids, cetaceans, proboscids and non-human primates, these mechanisms run in parallel with living–dead discrimination processes based on associative concepts. I've also argued that high-order reasoning skills such as inductive and/or analogical reasoning might be a *sine qua non* condition for human-like death awareness (Slaughter, 2005) with all of its main subcomponents (universality, irreversibility, cessation, and causation) which underpin its understanding, rather than just discriminating. Many authors have called for more and better data on animals' responses to the dead to advance comparative thanatology—greater taxonomic breadth, more quantitative descriptions and more systematic phylogenetic comparisons (Anderson, 2011; Watson & Matsuzawa, 2018; Reggentte et al., 2018). I also advocate for controlled experiments to probe the sensory and cognitive bases of the detection of death and its associated psychological states.

Chapter 4 - The study of emotions, particularly attributing grief to nonhuman animals, is a matter of ongoing debate, as many researchers emphasize either the unobservable nature of mental aspects of grief or the uniqueness of human grief and it being inextricably tied to the concept of death. However, considering grief is predominantly associated with behavioral and physiological changes in the individual (sleep disturbances, decreased social activity, decreased appetite, increased self-directed behaviors, stress hormone elevations), it is important to point out such changes have been documented both in humans and nonhuman primates (Anderson, 2011; Anderson, 2017; Gonçalves and Carvalho 2019). And although the majority of behavioral reports comes from nonhuman primates, there is convergent evidence from other animals including both mammals and bird species (King, 2013).

Chapter 5 - 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. 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 (Rosenson, 1977; Nakamitchi et al., 1996; Thompson et al., 2020), possibly due to postural/anatomical and behavioural constraints, the affective behaviours they exhibit towards their deceased infants are similar to other mammalian species. Dead adult and juvenile individuals engender greater attention from the group in comparison to dead infants (Stewart et al., 2012; Campbell et al., 2016; Porter et al., 2019) 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). 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. 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 (Gonçalves & Biro. 2018). 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 limited 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. The 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. 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 Pettitt, 2011) 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. 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 (Gonçalves & Carvalho, 2019).

Chapter 6 - Chimpanzees exhibit a variety of behaviors surrounding their dead ranging from several physical interactions to stationing around for extended periods and even revisiting the corpse (Anderson, 2018). Much less is known how they behave around conspecific skeletons (but see Watts, 2020). McComb and colleagues (2006), noticing wild elephants' natural propensity to interact with conspecific skeletons, measured their responses towards conspecific skulls and ivory. Their conclusions supported the notion that elephants are significantly more attentive towards conspecific stimuli. Following this line of research, I tested chimpanzees visual attention towards conspecific and non-conspecific skulls (cat, chimp, dog, rat), shown simultaneously in four corners of a screen in distinct positions (frontal, diagonal and lateral). Additionally, both faces and skull shaped stones of these animals were used following the same methods. The results showed that chimpanzees attended: (i) significantly longer towards conspecific skulls than other species skulls (particularly in forward-facing and to a lesser extent diagonal orientations); (ii) significantly longer towards conspecific faces than other species faces at forward-facing and diagonal orientations; (iii) longer towards chimpanzee faces compared with chimpanzee skulls and skull-shaped stones, and (iv) attended significantly longer to the teeth, similar to findings for elephant. These results suggest chimpanzee skulls still retain relevant, albeit impoverished, face-like features that arguably activate a domain specific face-module in the chimpanzee's brain, guiding their attention to them. Although, unlike wild chimpanzees, but perhaps notably, these captive subjects have never interacted with conspecific skeletons, this study proposes that, apart from learned, similar interest exhibited by wild chimpanzees towards conspecific skulls can be explained by the same recognition mechanism.

Chapter 7 - Since primates are primarily visual creatures, it was important to identify the key visual indicators of death. According to my outline, these include *inertia* (lack of movement), *injury* (severe disruptions of the body envelope), and *decay* (emaciation and putrefaction). Following it, I edited 20 image pairs of various animal species (terrestrial mammals) both alive and dead in a shared background for experiment 1 (condition a) to see if chimpanzees exhibit a visual living-dead attentional bias. I also edited 20 additional image pairs for this experiment (condition b) showing non-human primate mothers carrying both live and dead infants. Two aspects of looking patterns—latency to first look and fixation duration—were examined.

The findings of this study demonstrate that chimpanzees respond significantly more to images of live animals than to those of dead ones: they detected faster and looked significantly longer at images of live animals in comparison to death animals. These results are consistent with the *animate monitoring hypothesis* (New et al., 2007) and similar findings from other eye-tracking studies with humans using images of living (standing) versus living (lying down) animals, whether they be predators (lions) or prey (impalas), also consistent with this *animacy effect*, whereby subjects detect lifelike animals faster than dead-like animals (Yorzinski & Coss, 2020). This animate monitoring mechanism may be the cause of this *animacy effect* because live animals pose a more immediate threat, favoring built-in "quicker detection" and increased attention, as opposed to dead animals, which may be noticeable in the environment but do not require such active tracking because they lack agency cues. Future research could clarify where corpses fall along this hypothetical animacy continuum, allowing one to investigate how inanimate objects attract attention alongside dead animals or, conversely, what would happen if sleeping animals were placed next to dead animals (i.e. similar immediate monitoring for both but more prolonged monitoring for the sleeping animal) Although the *animacy effect* was demonstrated with primate-only stimuli for longer total looking durations (chimpanzees looked at live infant primates for longer), this was not the case for immediate monitoring (time/latency to the first fixation). One explanation is that infants who are still alive have more robust infantile cues that keep people's attention longer than infants who have died and are in various stages of decay. Other eye-tracking studies have revealed that chimpanzees look at live primate infants for noticeably longer when they are paired with their mothers (Kawaguchi et al., 2019).

## Concluding remarks: Answering Geza's Call

. Sometime before during the mid-1960s, Iain Douglas-Hamilton was passing through the southernmost region of the Manyara Park in Tanzania when he encountered an adult female (Torone Four) at the bottom of a slope, having fallen to her death. Next to her, were three calves standing vigil before abandoning the site. Over the next few days, he kept returning to this site to detail the process of decomposition and its effects on the soil. On the tenth, he spotted a rival group of elephants, its matriarch coming over and inspecting the body then followed by three other females. They exhibited a special interest in the tusks. This encounter prompted him to empirically test elephant's responses to carcasses, by placing elephant bones on two occasions separate occasions.

Douglas-Hamilton dedicated a whole section in his book to elephants' responses to death. This chapter, as accomplished as any review written today, details some first-hand reports and two pilot experiments, while also evaluating dozens of other cases and anticipating some of the current theoretical debate surrounding the function of thanatological interactions, stating near the end:

> *"Such responsiveness to inert bodies is of obvious value in saving a member of a group who has temporarily collapsed. The helpers may also later benefit from the sick animal's recovery when it resumes its role in the family unit's live.(...). A zoologist brought up in the theory of natural selection must always try to explain such apparently altruistic behaviour in terms of the helper's own advantage (...). What is far harder to explain in these rational terms is the value of the extraordinary interest which elephants sometimes show in corpses even when they are decomposed. (...) I have no idea why elephants carry bones. The special significance of the tusks (...) is mysterious, although of all the organs of the body they remain much the same in death as life, curving shafts of ivory, perhaps still with some signal effect. As with the burying behaviour, I shall know no more about it unless I, or someone else, conduct some controlled experiments designed to unravel exactly which stimuli elicit these responses, and then try to find out why. These phenomena are certainly not beyond the realms of experimental investigation. It is not enough to say that an elephant possesses a 'sense of death' and leave it at that."*

Douglas-Hamilton & Douglas-Hamilton [1975, *Among the Elephants*, pp. 103]

At roughly the same time and in the same country of Tanzania, Geza Teleki published his findings on the Gombe chimpanzees' responses to the accidental death of a group member (Rix), who fell from a tree. This remains one of the most detailed observations in the wild and the only one depicting the moment of death. It was in fact, the second scientific paper dedicated to this subject in chimpanzees since Arthur Brown's paper almost a century before. Teleki's conclusion is also worth quoting in full:

> *"The behavior of certain individuals in this episode seemed to indicate awareness of a change from activity to inactivity in a group member, but it remains uncertain whether any participant grasped the conceptual difference between life and death. (...) The combined responses of the group generated an atmosphere suggestive of greater insight, but the motives and results of the observed investigative behavior remain unclear in a field situation. In all possibility, unequivocal proof of such mental phenomena must be sought in captive situations, where cognitive capabilities can be precisely tested and verified. (...) Chimpanzee responses to death may provide another piece to the puzzle being assembled, for a potential to recognize the significance of death may have appeared long before Neanderthal men began to ritualize burial of their dead by the Middle Paleolithic."*

Geza Teleki [1973, *Folia Primatologica*, pp. 92-93]

It took 30 years for Iain's plea to finally be answered: manifested in a 2006 publication, undertaken in controlled experimental settings and substantiated by hard data. We now know that while elephants do show high levels of interest in their own-species skulls and particularly their tusks, they do not seem to differentiate them as belonging to particular individuals known to them in life.

There is a also compelling argument for some thanatological responses indicating attachment relationships and operating on the expectation the dead conspecific could recover.

Seemingly maladaptive, they may, however, serve an evolutionary purpose. By inspecting a corpse, socially bonded animals could be gathering information on the conspecific's state.

Only recently, as comparative thanatology is entering a data-driven and hypothesis-based stage, in which modern researchers are attempting to take on Geza's call to experimentally test chimpanzee's cognition of death-related stimuli (see Anderson et al., 2021). More empirical research being currently undertaken targeted at these and similar questions relating to grief and loss will be fundamental in expanding our knowledge of how non-human animals respond towards death.

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