



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

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1 **Death among primates: a critical review of non-human primate** 2 **interactions towards their dead and dying**

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17 18 **ABSTRACT**

19 For the past two centuries, non-human primates have been reported to inspect, protect, retrieve,
20 carry or drag the dead bodies of their conspecifics and, for nearly the same amount of time,
21 sparse scientific attention has been paid to such behaviours. Given that there exists a
22 considerable gap in the fossil and archaeological record concerning how early hominins might
23 have interacted with their dead, extant primates may provide valuable insight into how and in
24 which contexts thanatological behaviours would have occurred. First, we outline a
25 comprehensive history of comparative thanatology in non-human primates, from the earliest
26 accounts to the present, uncovering the interpretations of previous researchers and their
27 contributions to the field of primate thanatology. Many of the typical behavioural patterns
28 towards the dead seen in the past are consistent with those observed today. Second, we review
29 recent evidence of thanatological responses and organise it into distinct terminologies: direct
30 interactions (physical contact with the corpse) and secondary interactions (guarding the corpse,

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3 1 vigils and visitations). Third, we provide a critical evaluation regarding the form and function of
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5 2 the behavioural and emotional aspects of these responses towards infants and adults, also
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7 3 comparing them with non-conspecifics. We suggest that thanatological interactions: promote a
8
9 4 faster re-categorisation from living to dead, decrease costly vigilant/caregiving behaviours, are
10
11 5 crucial to the management of grieving responses, update position in the group's hierarchy, and
12
13 6 accelerate the formation of new social bonds. Fourth, we propose an integrated model of Life-
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15 7 Death Awareness, whereupon neural circuitry dedicated towards detecting life, i.e. the agency
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17 8 system (animate agency, intentional agency, mentalistic agency) works with a corresponding
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19 9 system that interacts with it on a decision-making level (animate/inanimate distinction,
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21 10 living/dead discrimination, death awareness). Theoretically, both systems are governed by
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23 11 specific cognitive mechanisms (perceptual categories, associative concepts and high-order
24
25 12 reasoning, respectively). Fifth, we present an evolutionary timeline from rudimentary
26
27 13 thanatological responses likely occurring in earlier non-human primates during the Eocene to the
28
29 14 more elaborate mortuary practices attributed to genus *Homo* throughout the Pleistocene. Finally,
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31 15 we discuss the importance of detailed reports on primate thanatology and propose several
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33 16 empirical avenues to shed further light on this topic. This review expands and builds upon
34
35 17 previous attempts to evaluate the body of knowledge on this subject, providing an integrative
36
37 18 perspective and bringing together different fields of research to detail the evolutionary,
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39 19 sensory/cognitive, developmental and historical/archaeological aspects of primate thanatology.
40
41 20 Considering all these findings and given their cognitive abilities, we argue that non-human
42
43 21 primates are capable of an implicit awareness of death.
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41 23 *Key words*: comparative thanatology, epimeletic behaviour, deceased infant carrying, deceased
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43 24 conspecific, concept of mortality, grief.
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- 53 30 **I. INTRODUCTION**
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1 Primate thanatology is the scientific study of the phenomenon of death and dying in non-
2 human primates, including the physiological, behavioural, social and psychological processes
3 associated with it (Anderson, 2017). Because non-human primates (henceforth primates) occupy
4 a close evolutionary trajectory to humans, they remain the best candidates to investigate how our
5 ancestors before the *Homo* lineage might have responded to death, preceding the emergence of
6 ritualised behaviours towards the dead – one of the defining traits of our species.

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

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

28 29 **II – PRIMATE THANATOLOGY: A SCATTERED HISTORY**

30 **(1) Early observations**

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3 1 The early 19th century was a period of great intellectual transformation. Europe
4
5 2 witnessed the rise of the first modern zoological gardens and natural history museums, the latter
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7 3 featuring wild specimens brought back from colonial territories (Hoage & Deiss, 1996;
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9 4 Burkhardt, 1999). In Paris at the *Jardin des Plantes*, Frédéric Cuvier was head of the *Menagerie*,
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11 5 where he kept living animals in confinement, believing them to be useful learning tools, akin to
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13 6 the dead animals in museums. These first attempts at keeping live animals were only partially
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15 7 successful as many died from disease or the harsher climate (Baratay & Hardouin-Fugier, 2003).
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17 8 Such was likely the fate of a common marmoset (*Callithrix jacchus*) whose bereaved companion
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19 9 Cuvier described as inconsolable before himself succumbing to death (Cuvier in Houzeau, 1872).
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21 10 Whilst travelling in India, James Forbes (1813) reported the shooting of a female monkey and
22
23 11 described how the troop responded by surrounding the gunman and advancing in a “menacing
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25 12 posture”, mentioning one particular male that “stood his ground, chattering and menacing in a
26
27 13 furious manner” before beginning a “lamentable moaning” and seeming to “beg” for the body
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29 14 (Forbes, 1813, p.17).

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31 15 It was with Charles Darwin that the notion of continuity between man and other animals
32
33 16 gained scientific credibility – although, despite musing over the possibility of other animals’
34
35 17 understanding of death, he credited only humans with an awareness of their own mortality
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37 18 (Darwin, 1871). Turning to something he could measure, Darwin published his writings about
38
39 19 the field of emotion, thoroughly detailing the mechanics of weeping, associating them with
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41 20 depressive states, and in so doing, linking the biological underpinnings of grief (Darwin, 1872).
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43 21 Arthur Brown (1879) published a report on a captive male chimpanzee’s (*Pan troglodytes*)
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45 22 behaviour following the death of its female “cagemate” – attempting to rouse the corpse, crying,
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47 23 and then whimpering. Richard Garner, in his endeavour to unlock the language of apes,
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49 24 witnessed two chimpanzees he had acquired die of illness and, through the reactions of the living
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51 25 ones, proposed that they must have an understanding of death (Garner, 1900).

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53 26 Through a comprehensive reading of these pre-ethological reports spanning from the 19th
54
55 27 to the early 20th centuries, we find three main patterns concerning primate behaviours towards
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57 28 their dead: (1) carrying/dragging corpses (Bowdich, 1819; Mollien, 1820; Kipling, 1891;
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59 29 Loveridge, 1923); (2) mobbing/defending corpses from attackers (Forbes, 1813; Johnston, 1885;
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30 Jenks, 1911; Reichenow, 1920; Aschemeier, 1921); and (3) apparent grieving over deceased
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32 companions (Houzeau, 1872; Brown, 1879; Sheak, 1917; Burbridge, 1928; Coolidge, 1933).

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3 1 Although anecdotal and tinged with naïve anthropomorphism, these reports rather accurately
4 describe behavioural patterns that are recurrent in present-day observations.
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8 4 **(2) Educated insights: Yerkes, Marais and Zuckerman**

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10 5 At the beginning of the 20th century, a second wave of accounts is characterised by
11 detailed reports from two intellectual descendants of Darwin: Robert Yerkes and Solly
12 Zuckerman. Yerkes reported the behaviour of a female rhesus macaque (*Macaca mulatta*) that
13 kept her dead infant for an extended period, interpreted as a manifestation of maternal instinct
14 (Yerkes, 1915). Later, Yerkes and his wife described the cognitive and emotional aspects of
15 apes, writing on the subject of grief and depression: it was “beyond dispute” that chimpanzees
16 underwent such emotional states (Yerkes & Yerkes, 1929).
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19 12 Eugène Marais, renowned for his pioneering field studies with chacma baboons (*Papio h.*
20 *ursinus*), described the behaviour of a captive female whose infant had been severely injured and
21 removed for treatment. She exhibited signs of distress, called continuously, and rarely ate for the
22 duration of her infant’s absence. When the dead infant was presented to her, she gave calls,
23 touched and sniffed it, but made no protest upon its removal, seemingly implying “a
24 comprehension of the significance of death and its consequence” (Marais, 1969, p.125).
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27 18 Zuckerman (1932) had a more conservative opinion. During his residence at London Zoo,
28 he observed a staggering number of violent interactions among hamadryas baboons (*Papio*
29 *hamadryas*), with more than two thirds of the troop dying from stress or injuries during a six and
30 a half year period and only one infant surviving out of the 15 that were born. Anticipating the
31 research of Harry Harlow, he spoke of an indiscriminate “reaction to fur” that orphaned baboon
32 infants showed, clinging to their mother’s fur after her death and being equally soothed by the
33 carcass of another dead baboon. Females were observed carrying their dead infants for days and
34 group members were fiercely opposed to the removal of a companion’s corpse. Males were also
35 observed copulating with female corpses. In Zuckerman’s view, that they would show these
36 behaviours regardless of whether the individual was alive, wounded or dead, was an indication of
37 their lack of awareness of death (Zuckerman, 1932).
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40 29 It is important to state that these observations were made in less than ideal captive
41 settings. In Yerkes’s case, the rhesus monkey was kept in a small cage that might have accounted
42 for an uncharacteristically long carrying period. Zuckerman’s observations were made within an
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3 1 artificial population of individuals, during an event now dubbed the “Monkey Hill Massacre”,
4 2 resulting from a lack of knowledge of *Hamadryas* baboon social organisation (Zuckerman,
5 3 1932). Similar miscalculations led to a violent reorganisation within the introduced rhesus group
6 4 on Cayo Santiago, Costa Rica (Carpenter, 1959).
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10 5 11 12 6 **(3) Initial field reports**

13 7 Most reports from the field took the form of side notes to larger research agendas (Kawai,
14 8 1960; Booth, 1962; Jay, 1962; Schaller, 1963; DeVore, 1963; Koford, 1965; Bernstein, 1968;
15 9 Struhsaker, 1971; Mittermeier, 1973), with notable exceptions (Teleki, 1973; Nash, 1974;
16 10 Mohnot, 1980). Jane Goodall described several chimpanzee reactions towards dead and dying
17 11 conspecifics, many occurring during an outbreak of Polio (van Lawick-Goodall, 1968, 1971;
18 12 Goodall, 1986). One female (Olly) started carrying her infant in unusual fashions (slung over her
19 13 shoulder, by the arm or leg) once he stopped showing signs of life, whilst in marked contrast
20 14 another female (Mandy) still carried her dead infant ventrally. Goodall noted their “dazed”
21 15 expressions (van Lawick-Goodall, 1968), later commenting on their possible awareness of their
22 16 infant’s deaths (van Lawick-Goodall, 1971). There were also reports of an adult female (Honey
23 17 Bee) caring for her fatally injured mother, and the grief-like reaction of a juvenile (Flint) to the
24 18 death of his mother (Flo), himself dying days later (Goodall, 1986).
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34 19 Despite some authors arguing that such behaviour was non-adaptive, others speculated
35 20 that it may be evolutionarily advantageous, particularly for mothers carrying temporarily
36 21 immobilised infants – a behaviour proposed to be selected for in species with low reproductive
37 22 rates, such as primates (Alley, 1980).
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43 24 **(4) Experimental/quasi-experimental research**

44 25 The emerging subfield of primate thanatology was not outside the experimental sphere.
45 26 Besides key studies exploring grief-like responses using the *infant-mother separation paradigm*
46 27 (Jensen & Tollman, 1962; Seay, Hansen & Harlow, 1962; Hinde, Spencer-Booth & Bruce, 1966;
47 28 Kaufman & Rosenblum, 1967), other experimental paradigms included: the *stuffed/fresh corpse*
48 29 *paradigm* (Hebb, 1946; Butler, 1964, Bertrand, 1969; Kaplan, 1973), where a recently
49 30 dead/stuffed primate was introduced to the group; the *anaesthesia paradigm* (Rosenblum &
50 31 Youngstein, 1974; Rosenson, 1977; Negayama, 1988), involving the presentation of a live but
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1 temporarily inert individual; the *playback call paradigm* (Allen & Hauser, 1991; Palombit,
2 Seyfarth & Cheney, 1997), whereby calls of dead infants or their mothers are played to group
3 members; and the *hormonal paradigm* (Engh *et al.*, 2006; Kaplan, Pines & Rogers, 2012;
4 Seyfarth & Cheney, 2013), which measures stress levels through sample collection upon the
5 death of a group member.

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

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

27 **(5) Current views**

28 Published accounts on primate thanatology have been increasing in number (Fig. 1).
29 Recent decades have yielded reports from Japanese (Negayama, 1988; Kano, 1992; Yoshida,
30 1994; Nakamichi, Koyama & Jolly, 1996; Matsuzawa, 1997; Hosaka *et al.*, 2000; Kooriyama,
31 2009; Sugiyama *et al.*, 2009), Chinese (Lu, Zhao & Li, 2007; Chen & Li, 2011; Li *et al.*, 2012;

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3 1 Chai *et al.*, 2013; Yang, Anderson & Li, 2016; Guo *et al.*, 2016) and Indian (Rajpurohit, 1997;
4 2 Balasubramanian & Sabu-Jahas, 1997; Gupta, 2000; Sharma *et al.*, 2011) primatologists, in a
5 3 field previously dominated by British and American researchers.

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7 4 If ever a picture was worth a thousand words, then certainly the image printed in the
8 5 November 2009 edition of National Geographic Magazine showing a dead chimpanzee being
9 6 carried away in full view of her silent community members was the case (Speede, 2013). The
10 7 story renewed interest in the matter of death awareness in non-human animals. Soon after, key
11 8 papers published on the subject (Anderson, Gillies & Lock, 2010; Biro *et al.*, 2010; Fashing *et*
12 9 *al.*, 2011; Cronin *et al.*, 2011) sparked both curiosity and controversy – particularly Anderson *et*
13 10 *al.* (2010) whose claims that the chimpanzees were checking for signs of life and possibly
14 11 attempting to resuscitate their deceased group member were met with criticism and termed
15 12 anthropomorphic (Semple *et al.*, 2010; Penn, 2011), as well as inciting recommendations of
16 13 cautious interpretation (Barrett, 2012). Over the years, many scholars have given credence to the
17 14 possibility of chimpanzees having an awareness of death (de Waal, 1996, 2013; Gallup, 1998;
18 15 Bering, 2001; Boesch, 2012). Conversely, because they greet each other but do not communicate
19 16 goodbyes, it has been contended that, at a profound cognitive level, they may lack awareness of
20 17 mortality (McGrew & Baehren, 2016).

21 18 However, these statements currently stand on the confines of uncontrolled observation,
22 19 with its strengths and limitations, on a phenomenon that is ultimately rarely witnessed in long-
23 20 lived animals. As claimed by Bering, “ethological reports must — for now — suffice as our only
24 21 window through which to glimpse this very interesting topic. But it is a window with a good
25 22 view.” (Bering, 2001, p.124).

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24 III. PRIMATE THANATOLOGY: CONTEMPORARY REPORTS

25 (1) Dead infants

26 Females of several primate species have been observed persistently to carry their
27 27 deceased infants (sometimes for prolonged periods of 10 days or more), regardless of the
28 28 circumstances that caused the fatality (Fig. 2). Other recorded behaviours include grooming,
29 29 swatting flies away from the corpse and sometimes even consuming part of it. Primatologists
30 30 have described their expressions as “puzzled”, “confused” or “dazed”, which raises the question
31 31 as to whether they have some, if any, understanding of death.

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4 1 These behaviours are striking because they seem maladaptive. Whilst live infants are
5 2 energetically costly to the mothers who carry them, ultimately they increase reproductive fitness
6 3 – something a dead immature offspring cannot do. Holding a lifeless corpse hinders locomotion,
7 4 negatively impacting foraging and predator avoidance. Some will solve these difficulties by
8 5 adopting a tripod gait, carrying the corpse ventrally, using the neck and shoulder to wedge it,
9 6 drag it along the ground, or even carry it dorsally using the tail as an extra limb. While some
10 7 hypotheses have been proposed to explain post-mortem carrying (Table 1), it is still a matter of
11 8 debate which one offers the most powerful explanation. Because some are mutually non-
12 9 exclusive it is likely that many factors, depending on context, contribute to these behaviours (see
13 10 Watson & Matsuzawa, 2018).

11 12 (a) *Mother–infant dynamics*

13 14 Dead-infant carrying is the most prevalent thanatological behaviour distributed in several
15 15 primate taxa (Fig. 3). This should not be surprising since: (1) primates follow a typical trend
16 16 observed in many vertebrate species of high infant mortality (Bronikowski *et al.*, 2011); and (2)
17 17 unlike adolescents and adults who are abandoned at their site of death, dead infants and juveniles
18 18 are usually carried by the mother for longer durations, allowing easier detection. Nevertheless,
19 19 the mother will, invariably, cease to carry the corpse, leaving it unattended for progressively
20 20 longer periods until finally abandoning it (Jay, 1962; Nash, 1974; Green, 1975; Altmann, 1980;
21 21 Hosaka *et al.*, 2000; Cronin *et al.*, 2011).

22 22 Many authors have claimed that the mother ceases to treat her infant as a live one during
23 23 this period – carrying it in awkward positions, by the leg or tail, upside down, using the mouth or
24 24 dragging the corpse along the ground (van Lawick-Goodall, 1968; Green, 1975; Altmann, 1980;
25 25 Lu *et al.*, 2007; Perry & Manson, 2009; Biro *et al.*, 2010; Fashing *et al.*, 2011). Green (1975),
26 26 who conducted a comprehensive vocal study with wild Japanese macaques (*Macaca fuscata*),
27 27 noted that mothers gave out particular vocalisations when their infants died, repeated whilst
28 28 carrying the infant or distant from it. Some have proposed that infantile colouration may elicit
29 29 *post-mortem* carrying (Jay, 1962; Alley, 1980; Rajpurohit, 1997), but this does not explain why
30 30 such behaviour occurs in females from myriad primate species – some with flamboyant natal
31 31 coats and others non-conspicuous.

1 Perry & Manson (2009) describe a case of a capuchin female (*Cebus capucinus*) carrying
2 her stillborn, arguing that she behaved in ways which suggested an awareness of her infant's
3 death, such as letting the infant be fully submerged in water. Although this could represent
4 causal attribution, it may equally be a failure of perspective taking. Inexperienced Japanese
5 macaque mothers have been observed to inadvertently drown their infants when diving into the
6 hot springs of Jigokudani Park for food (de Waal, 1996) and similar occurrences have been
7 reported among baboons (Cheney & Seyfarth, 2007). Moreover, filial cannibalism during *post-*
8 *mortem* carrying has also been witnessed, suggesting that corpses may be re-categorised as food
9 (Altman, 1980; Hsiang-Jen & Hsiu-Hui, 2008; Dellatore, Waitt & Foitova, 2009; Watson *et al.*,
10 2015; Tokuyama *et al.*, 2017; Tian *et al.*, 2016; De Marco, Cozzolino & Thierry, 2018; Watson
11 & Matsuzawa, 2018).

12 Cronin *et al.* (2011) propose that whilst displaying approach–withdrawal behaviour
13 towards the infant, the mother is actively gathering novel death cues that she could conceivably
14 recall in equal situations (i.e. death of another conspecific). However, if the purpose of such
15 knowledge is to prevent costly behaviours, findings from Sugiyama *et al.* (2009) that there is no
16 significant difference in carrying duration between younger and older mothers suggests that, at
17 least in Japanese macaques, no such learning component was found. Moreover, reports on
18 chimpanzees from Bossou illustrate that there may be an individual component. Of the five
19 infants that died during a flu epidemic, only two were carried for extended periods (Biro, 2011).
20 Jire transported both her dead infants: Jokro in 1992 and again Jimato in 2003 (Matsuzawa,
21 1997; Biro *et al.*, 2010). Similarly, in semi-ranging Japanese macaques, the same female was
22 reported carrying her dead infant for extended periods in 2011 and again in 2013 (Watson *et al.*,
23 2015), although other factors such as cause of death could impact these responses (see Section
24 III.1e).

25 26 (b) Group–infant dynamics

27 The behaviour of group members who were not emotionally involved with the infant is
28 also of interest. Cheney & Seyfarth (2007) note that wild chacma baboons (*Papio h. ursinus*) do
29 not attempt to handle dead infants and rarely grunt at them as they would live infants. Similarly,
30 Rajpurohit (1997) mentions that in Hanuman langurs, other members show little interest in dead
31 infants – a finding also reported in other species (van Lawick-Goodall, 1968; Green, 1975; Lu *et*

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3 1 *al.*, 2007; Guo *et al.*, 2016; de Marco *et al.*, 2018). Conversely, infants and juveniles express
4 2 more interest in the corpse (van Lawick-Goodall, 1968; Ciani, 1984; Cronin *et al.*, 2011; Li *et*
5 3 *al.*, 2012), some even playing with it (van Lawick-Goodall, 1971; Hosaka *et al.*, 2000; Biro,
6 4 2011). Furthermore, juvenile and nulliparous adult females have been witnessed carrying dead
7 5 infants relinquished by their mothers (Warren & Williamson, 2004; Fashing *et al.*, 2011). The
8 6 mother occasionally restricts attempts by other group members to access the corpse (Altmann,
9 7 1980; Gupta, 2000; Li *et al.*, 2012; Tokuyama *et al.*, 2017) (Fig. 4), with siblings having broader
10 8 admittance (van Lawick-Goodall, 1971; Kano, 1992; Muller *et al.*, 1995; Matsuzawa, 1997). It is
11 9 conceivable that such playful interactions may prepare younger individuals for death recognition.

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

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

(c) *Old World–New World dichotomy*

To the best of our knowledge, there are 13 published cases of dead-infant carrying among New World monkeys, comprising cebids, and atelids (see online Supporting information, Appendix S1). The lack of information on this behaviour may be partly due to the smaller

1 number of publications on New World primates. Anderson (2011) argues that their tropical
2 habitats accelerate the decay of corpses and consequently their abandonment. Additionally, while
3 Old World monkeys can be either arboreal, terrestrial or both, New World monkeys are almost
4 exclusively arboreal (Fernandez-Duque, Di Fiore & Huck, 2012). Referring to an arboreal Old
5 World species, the red colobus (*Piliocolobus tephrosceles*), Struhsaker (2010) pointed out the
6 difficulty of carrying a dead infant while leaping between trees – a claim supported by other
7 colobine cases (*Colobus guereza*: Onderdonk, 2000; *Colobus vellerosus*: Teichroeb & Sicotte,
8 2008) and the observation that species that carry their dead for long periods, such as snub-nosed
9 monkeys (*Rhinopithecus bieti*) tend to be more terrestrial (Long & Kirkpatrick, 1994). Observer
10 bias may also be involved; when reviewing the literature on post-mortem carrying, the best-
11 represented species were semi or fully terrestrial and inhabited accessible areas or were in close
12 proximity to human communities (Sugiyama *et al.*, 2009; Rajpurohit, 1997; Fashing *et al.*,
13 2011). The only case of dead-infant carrying recorded among prosimians comes from ring-tailed
14 lemurs (*Lemur catta*) (Nakamichi *et al.*, 1996), the most terrestrial lemur (Schmidt, 2011).

15 16 (d) *Non-carriers*

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

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3 1 (*Otolemur crassicaudatus*) retrieved her infant using her jaws (later and dropping it when
4 attempting to groom), and a black lemur (*Eulemur macaco*) was seen gripping and lifting her
5 infant. Grooming was observed in all mothers, most of which were in regular contact with their
6 infants, likely representing an attempt to elicit a response. While it seems strepsirrhines lack the
7 morphological proficiency for extended periods of carrying, their behaviour suggests they are not
8 indifferent to their dead or dying infants, even after they stop showing signs of life (Nakamichi,
9 2016).

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15 8 Callitrichines are not known to engage in dead-infant carrying, apparently relying on life
16 cues such as movement and vocalisations to initiate carriage, consequently, care of stillborn and
17 weak infants ceases rapidly (Rothe cited in Price, 1990). These primates have uncommon
18 features among anthropoids as they have undergone phyletic dwarfism, possess tegulae (claw-
19 like nails), regularly give birth to twins, and the males are the primary carriers of infants
20 (Fernandez-Duque *et al.*, 2012). Whilst there are no reports of callitrichines successfully carrying
21 dead/dying infants, short-lived attempts can occur, with group members smelling, grooming,
22 swatting flies, and scent-marking the infant, before ultimately abandoning it to re-join the group
23 – an ambiguous behavioural repertoire, similar to that seen with lemurs (Digby, 1995; Roda &
24 Pontes, 1998; Lazaro-Perea *et al.*, 2000; Hilário & Ferrari, 2010; Culot *et al.*, 2011). Detailed
25 observations by Thompson *et al.* (2018) emphasise these patterns: failed attempts to carry the
26 corpse by a male and a female, several visits to the body by group members which decreased
27 over time, and general group interest in the corpse sustained for over 2 h with one adult male
28 remaining in an apparent vigil after the rest of the group left (see Section III.2c).

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39 22 The explanation for these observations may lie both in the general anatomy of these
40 species and in their behavioural adaptations that preclude long-term dead-infant carrying (i.e.
41 mothers do not hold newborns as the infants grab onto their fur, and unlike other anthropoids
42 these species do not engage in bipedal carriage) (see also Rumbaugh, 1965).

43 44 45 46 47 48 27 (e) *Contextual and sensory cues to death*

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50 28 Non-human primates face death from a variety of causes ranging from predation,
51 conspecific attack, accidental falls, disease, starvation and stillbirth. Infants may be carried *post-*
52 *mortem* regardless of the cause (Fig. 5). Anderson (2011) claimed that distinct contexts of death
53 could elicit different treatment from the living. Although it remains challenging for
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3 1 primatologists to record an actual moment of death, extensive records spanning decades exist for
4 cases of infanticide (see Appendix S1 and S3). The primary mode of death in these cases is often
5 a cranio-cervical bite (King & Steklis, 1984, 2008), leaving visible wounds to the head and spine
6 region. Infanticide is of particular interest because (1) it affords a contextual cue (a causal chain
7 of events leading to the death of the infant witnessed by the mother and other group members)
8 and (2) it offers strong sensory death cues (i.e. visual cues of wounds).
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13 7 Das *et al.* (2018) found that carrying duration in cases of infanticide was significantly
14 lower in comparison to other causes of death. They attribute three subcomponents typical of
15 human death awareness (see Table 2) to mothers carrying dead infants: repeated sensory
16 investigation as a result of having ‘Causation’, handling of the inanimate infant and its defence
17 as understanding ‘Cessation’, and progressive disinterest as possessing ‘Irreversibility’. Their
18 claim, however, fails to account for primate mothers exhibiting the same behaviours in other
19 contexts. Grooming is a widespread thanatological response likely related to interest but it occurs
20 repeatedly days after any potential causal relation was made. Defence and abandonment also
21 occur with live infants.
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29 16 Reviewing 59 cases of observed infanticides in New World and Old World primates, we
30 found that about a third of the infants were carried by their mothers ($N = 20$) (see Tables S1.1.,
31 S1.2. and S1.4 of Appendix S1), compared to two-thirds that were not ($N = 39$) (Appendix S3).
32 This finding supports the results of Das *et al.* (2018) and suggests that contextual and sensory
33 death cues aid the mother’s understanding of the infant’s condition, allowing her to terminate her
34 parental investment. Surprisingly, in 14 cases, infants were abandoned alive after being injured
35 by an infanticidal male. During group takeovers, Hrdy (1974) reports that Sugiyama (1967) and
36 Rudran (1973) interpret such cases as the mother fearing injury from the male. Nonetheless Hrdy
37 (1974) proposed that such desertions represent a practical evaluation of the infant’s condition by
38 the mother weighing the current infant’s survival chances against those of a new offspring sired
39 by the incoming male. While she did not discuss any psychological mechanisms, it is highly
40 likely on a proximate level that such decisions, through associative learning or higher cognitive
41 mechanisms, are supported by contextual and physical cues of both injury and death. Other
42 situations offering comparable sets of cues including predation (Matsuda, Tuuga & Higashi,
43 2008), mishandling and electrocution (Das *et al.*, 2018) also lead to *post-mortem* infant
44 desertion.
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(2) Dead group members

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

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

(a) Direct interactions

There are relatively few reports of responses to dead juveniles and adults, with most involving chimpanzees where responses range from peaceful to aggressive (Appendix S4). Besides peering, they may engage in gentle physical contact, such as inspecting, grooming,

1 poking and sniffing, thus obtaining tactile and olfactory information on the state of the dead
2 individual, and possibly attempting to elicit a response. As with dead infants (Goodall, 1977;
3 Matsuzawa, 1997; Cronin *et al.*, 2011; Biro, 2011), attention is directed towards the head or face
4 (Box, 1984; Anderson *et al.*, 2010; Buhl *et al.*, 2012; van Leeuwen *et al.*, 2016).

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

11 Such contacts have been interpreted as attempts to rouse the dead or as expressions of
12 frustration in chimpanzees (Anderson *et al.*, 2010; Westoll, 2011). Galdikas (cited in Thompson,
13 2009) described a curious case of an orphan orangutan (*Pongo pygmaeus*) that killed two
14 conspecifics and attempted to kill a third through drowning. On one occasion, he was observed
15 shaking the hands of the dead orangutan as if trying to stimulate a response (for similar
16 behaviours see Bygott, 1972; Sabater-Pi *et al.*, 1993). Galdikas believed he was experimenting
17 with life and death and seemed to appreciate the difference between these states.

18 Other cases seem to indicate attempts to monopolise the corpse and incorporate it in
19 aggressive displays (Fossey, 1983; Stewart *et al.*, 2012; Buhl *et al.*, 2012). Copulations and
20 mountings have been documented in these contexts directed at the corpse (Bertrand, 1969;
21 Bezerra *et al.*, 2014) and among group members (Teleki, 1973; Buhl *et al.*, 2012; Pruett *et al.*,
22 2017). Many responses also appear to be compassionate; Bezerra *et al.* (2014) describe a wild
23 common marmoset male exhibiting emotional/caretaking behaviours towards its dying mate such
24 as alarm calling, embracing, sniffing and protecting the corpse. Other behaviours such as
25 attempting to copulate as opposed to testing for a response could signify high levels of arousal.

26 Interactions may also include objects which are employed in different contexts. One
27 report described a chimpanzee engaging in “corpse cleaning”, and suggested that this was both a
28 socially meaningful way of handling the corpse and an attempt to learn about its state (van
29 Leeuwen, Cronin & Haun, 2017; see also “investigatory probing” in McGrew, 2004, p. 124).
30 After the death of a female lowland gorilla, King (2013) describes the male placing celery (her
31 favourite food) on her hands. In a chimpanzee sanctuary, after a dead female was presented to

1 her group, they groomed and attempted to tickle her, before her body was dragged and shaken by
2 a male who, in the process, caused her face to seep blood, which was then wiped off with paper
3 towels by another female (Westoll, 2011). Boesch (2012) detailed how leafy branches are
4 dropped onto chimpanzee corpses, sometimes covering the bodies. He cautioned against
5 interpreting these as “burial behaviors”, since chimpanzees have been observed to do this with
6 other dead animals, perhaps as a way to test if the body is moving. Furthermore, several monkey
7 and ape species drop tree materials on other species, including humans, in agonistic contexts
8 (Shumaker, Walkup & Beck, 2011). Some interactions are more violent; after the intragroup
9 killing of a chimpanzee male, Pruett *et al.* (2017) describe rocks being thrown at the corpse by
10 two individuals and a third hitting it repeatedly with a stick.

11 12 (b) *Guarding the body*

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

24 Guarding the body from other group members, defined as higher-ranking individuals
25 impeding close examination of the corpse by younger/lower-ranking individuals, is exhibited in a
26 few primate species. Tina, a chimpanzee killed by a leopard, was observed being guarded by
27 three adult males and a high-ranking female (who were not particularly bonded with her in life)
28 in an interaction that lasted for six hours (Boesch, 1991). Lower ranking individuals were
29 generally chased away, with the exception of Tina’s younger brother. Bezerra *et al.* (2014),
30 observing common marmosets, described the group’s alpha male guarding the body of his dead
31 mate while alarm calling and assuming a defensive posture, preventing juveniles and infants

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3 1 from approaching the corpse. Guarding the mother of a dead infant has been recorded in
4 chimpanzees (Boesch & Boesch-Achermann, 2000) and in Gelada baboons, where a male
5 2 guarded a mother with her dead infant from an infanticidal male (Mori, Iwamoto & Bekele,
6 3 1997). Occasionally among baboons, close relatives/male friends have been observed to guard an
7 4 infant's body while the mother forages, and individuals will band together to defend the corpse
8 5 (Cheney & Seyfarth, 2007). Guarding responses share behavioural traits with sympathetic
9 6 concern and empathetic targeted helping (Pérez-Manrique & Gomila, 2018), and appear to be
10 7 part of an evolved set of compassionate responses derived from neurophysiological mechanisms
11 8 dedicated towards mother–infant bonding and cognitive mechanisms involved with kin-based
12 9 and alliance-based based associations (reviewed in Gilbert, 2015).
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12 (c) *Vigils*

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

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

11 Visitations are defined as returns to the place where death ensued or the corpse was last
12 seen. Such places may hold residual information about the event which can arouse curiosity or
13 emotional distress. Smuts (1985) describes how, in the weeks following the infanticide of a
14 yellow baboon, the bereaved mother (Zandra) became extremely agitated and called when
15 passing the site of death, apparently initiating a search for her dead infant. In captive pottos
16 (*Perodicticus potto*), Cowgill (1972) reported a surviving couple searching for a dead male in its
17 usual sleeping site following its removal from the cage, and leaving portions of food, presumably
18 for the absent male (according to the author) – a behaviour maintained even when the portion
19 size was reduced. Following the cagemate's removal, the surviving pottos may have suffered a
20 decrease in appetite, suggesting a grief-like response (see Section III.3b). Similar searches have
21 been described in chimpanzees when no corpse was visible (van Lawick-Goodall, 1971). Perry
22 & Manson (2009) describe capuchins, after the removal of a dead infant, alarm calling at site
23 where the corpse was previously seen (see also Riley, Koenig & Gumers, 2015). Chimpanzees,
24 gorillas, long-tailed macaques (*Macaca fascicularis*) and hanuman langurs have been observed
25 returning to the place where a body was last seen and inspecting the ground (Mohnot, 1980;
26 Prince-Hughes, 2001; Stewart *et al.*, 2012; Pruetz *et al.*, 2017). If the corpse is not removed,
27 chimpanzees may revisit it the following day (Fawcett & Muhuzuma, 2000). Returning to a
28 corpse has been recorded for wild lowland and mountain gorillas at three different sites (Robbins
29 *et al.*, 2016) and captive marmosets (Box, 1984). The chimpanzee Flint, soon after the death of
30 his mother Flo, spent two minutes staring at a nest they had shared prior to her death. Later, he
31 returned to the place where Flo had died and “sank deeper into depression”, before his final

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3 1 excursion to the site, where he “curled up” and died (Goodall, 1990, p. 197). Patricia Wright
4 (cited in Safina, 2015) reports on a family of sifakas that, after predation of the adult male, gave
5 2 out lost calls and visited the corpse 14 times in five days. While some of these events may
6 3
7 4 simply indicate curiosity and an attempt to obtain information on the death event, others
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9 6 illustrate continuation of emotional bonds after death that were maintained during life.

10 7 Avoidance of the death sites of conspecifics, has also been observed in captive
11 8 chimpanzees (Anderson *et al.*, 2010; E. Ichino, 2018, personal communication), although this
12 9 has not yet been observed in the wild (Piel & Stewart, 2015; but see Pruett *et al.*, 2017). At the
13 10 very least, this implies some comprehension that a significant event took place that carries
14 11 negative emotional valence and possibly represents danger. Analogous responses have occurred
15 12 in wild yellow baboons, anubis baboons (*Papio anubis*), chacma baboons and rhesus macaques
16 13 where, following severe disturbance (trapping or predation events), groups abandoned their
17 14 sleeping sites (reviewed in Anderson, 1984; Matsumoto-Oda, 2015). By contrast, Mohnot
18 15 (1971) describes the decimation of a group of langurs in which 72 individuals died within the
19 16 space of three days, possibly due to contaminated water, leaving only 11 survivors. Despite their
20 17 decaying group mates being scavenged by crows and vultures and the foul odour present,
21 18 surviving members continued to return to the site. It is possible that witnessing the gradual
22 19 deaths of group members without any observable causation (i.e. predation) might have impacted
23 20 their behaviour (for fearful responses to abrupt deaths see Teleki, 1973; Boesch, 2012).

21 (3) Grieving/stress patterns

22 22 Grief is an emotional response triggered by loss and characterised by active distress and
23 23 passive depression, universal in human cultures but also seen in social mammals and some birds
24 24 following the loss of a parent, mate or offspring (Archer, 1999). Explanatory hypotheses include
25 25 a by-product of attachment, group cohesion, a death reminder, and an honest signal of
26 26 commitment (reviewed in Winegard *et al.*, 2014). Whatever the proximate/ultimate causation, it
27 27 is clear that grief is primarily caused by the severance of social bonds, such as the death of a
28 28 significant individual, and that grieving states described in the primate literature have a
29 29 substantial resemblance to human grief (Sapolsky, 2016; Anderson, 2017).

30 30 Seminal studies on mother–infant separation in macaques (Jensen & Tolman, 1962; Seay
31 31 *et al.*, 1962; Hinde *et al.*, 1966; Kaufman & Rosenblum, 1967) did much to illustrate the

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3 1 emotional and behavioural responses to separation in infants. These studies described two stages:
4 2 protest (categorised by marked increases in movement and vocalisation) and despair (substantial
5 3 reduction in activity and intensification of self-directed behaviours). These stages were
6 4 accompanied by alterations in body temperature, heart rate, endocrinal/immune system and
7 5 neurochemistry, together with decreases in food and water intake, and in some cases were
8 6 followed by death (Spencer-Booth & Hinde, 1971; Gilmer & McKinney, 2003).
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15 8 (a) *Orphans*

17 9 A few observations have detailed how infant and juvenile primates respond to the death
18 10 of their mother. Mohnot (1980) describes a 28-week-old langur vocalising in visible acute and
19 11 prolonged agitation whilst in physical contact with the corpse. Fashing *et al.* (2011) describe an
20 12 orphan gelada (Tussock) vocalising and rocking beside her dead mother away from the rest of
21 13 the group; she died the following day. Goodall (1986) outlined the behavioural changes of nine
22 14 orphaned chimpanzees, including lethargy, decreased play, loss of appetite, and emaciation. The
23 15 most severe case was of Flint who was considerably attached to his mother and, after her death,
24 16 fell into a depressive state, that ended in his death three weeks later (Goodall, 1990). Goodall
25 17 (1990) also recounts the case of the juvenile Pax who became agitated and screamed following
26 18 his mother's (Passion) death, constantly pulling her hand and carrying out a vigil with his two
27 19 elder siblings, moving away before nightfall. Successful adoptions have a positive effect, as seen
28 20 in a captive orangutan that spent more time in physical contact with her aunt after her mother
29 21 died and showed no significant self-directed behaviours (Whilde & Marples, 2011).
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41 23 (b) *Group companions*

43 24 The loss of an infant may trigger a grief response in the mother. De Waal (1996) vividly
44 25 illustrates the case of a captive chimpanzee that whimpered and wailed after the loss of her infant
45 26 (see also Blair, 1920). The wild chimpanzee Pom, after the death of her infant from an accidental
46 27 fall, became lethargic and emaciated to a life-threatening point, eventually readjusting by
47 28 developing a closer relationship with her own mother (Goodall, 1990). In chacma baboons,
48 29 recording a total of 26 deaths, Engh *et al.* (2006) reported that stress levels were particularly high
49 30 for females who had lost a relative when compared to control females. These "bereaved" females
50 31 seemed to compensate by widening and reinforcing their grooming network, which the authors
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1 suggest would have returned their stress levels to baseline. Additional research on these baboons
2 found temperamental differences impacting the success of friendship formation after the death of
3 a relative (Seyfarth & Cheney, 2013). Likewise, Kaplan *et al.* (2012) recorded a more than
4 doubling in stress levels in a group of common marmosets following the accidental death of a
5 roommate; stress levels remained high for 3 days. Despite not observing overt signs of grief,
6 Fossey (1983) reported similar readjustments (playing with juveniles) in primiparous female
7 mountain gorillas whose infants were subject to infanticide, perhaps, the author suggests,
8 strengthening social ties. In captive lowland gorillas, after the loss of the dominant male
9 (silverback), both mother–infant bonds and female–female aggression intensified (Hoff, Holt &
10 Marple, 1998). Self-directed and other behaviours indicative of stress also increased in two
11 captive gorilla populations (Less *et al.*, 2010). In captive siamangs (*Symphalangus syndactylus*),
12 Orgeldinger (1996) reported significant behavioural changes in the male and female of a pair
13 following the death of their infant, with increased levels of play, bonding, and sexual and
14 agonistic behaviours and decreased territorial behaviours. Majolo & McFarland (2009) report
15 self-suckling in wild Barbary macaques after the loss of their infants, suggesting that it may have
16 a stress-releasing function.

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

29
30 (c) *Grief and awareness*

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3 1 Grief by itself does not presuppose an awareness of death. Despite many thanatological
4 reports, primates have seldom been witnessed comforting grieving group members (Cheney &
5 2 Seyfarth, 1990, 2007). Box (1984) reports the death of a captive female common marmoset in
6 3 which the male spent time grooming her and scent marking. After the body was removed the
7 4 eldest daughter groomed her father attentively in addition to scent marking. In her behaviour she
8 5 seemed to be assuming the role of her dead mother. While the male protested at the removal of
9 6 the corpse, within minutes, he and the whole group became calm. An account describing how a
10 7 young Japanese macaque female clutching her dead infant and wailing was embraced by her own
11 8 mother illustrates the difficulty of interpreting such events as consoling (Green *in* Pierotti &
12 9 Annett, 2014). Yoshida (1994) describes a captive group of chimpanzees staying in close
13 10 proximity to a bereaved mother for longer durations than usual and grooming her. Mohnot
14 11 (1980) also reports three adult hanuman langur females intercepting an agitated orphan,
15 12 embracing him and preventing him from approaching his dead mother.
16 13

17 14 Naturally, single observations such as these do not allow us to ascribe motivation to the
18 15 consoler concerning the griever's state. The most parsimonious explanation in some if not all
19 16 cases is that the consolers simply respond to the subject's emotional state, regardless of any
20 17 causal attribution to their condition. Empathy does not operate solely on cognitive levels, at its
21 18 basis being a spontaneous emotional contagion response (see de Waal, 2008).
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23 20

24 20 **(4) Interactions with dead non-conspecifics**

25 21 Primates share their habitats with other species. Thus, it is of interest to consider whether
26 22 there are differences between their responses to a corpse of their own species compared to
27 23 another species. Do their responses fall on an animacy continuum, where phylogenetically close
28 24 groups elicit more similar responses than those for phylogenetically distant groups? Preliminary
29 25 data suggest that adult-sized and infant-sized mammal non-conspecifics elicit similar responses
30 26 in primates to adult and infant conspecifics, respectively. In wild yellow baboons, Hausfater
31 27 (1976) observed a nulliparous female carrying a dead rat clutched to her ventrum until it was
32 28 snatched by two juveniles who licked it, and another female who attempted to groom it (see also
33 29 Loveridge, 1921). In wild chimpanzees, analogous responses were seen in a young female
34 30 towards dead rodents (van Lawick-Goodall, 1968), and similar behaviours have been reported in
35 31 females carrying a limb of a dead colobus (*Procolobus rufomitratu*s) and dead hyraxes
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3 1 (*Dendrohyrax dorsalis*) (Hirata *et al.*, 2001; Cibot, Sabiiti & McLennan, 2017). Another case
4 2 included an old female bonobo carrying a dead red-tailed monkey (*Cercopithecus ascani*) for 43
5 3 days (Toda, Tokuyama & Furuichi, 2017). Additionally, in Barbary macaques, males have been
6 4 observed using dead rabbits in triadic male interactions in place of infants (Turckheim & Mertz,
7 5 1984).

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10 6 Some cases refer to ‘animal toying’ in great apes (Boesch & Boesch, 1989; Zamma,
11 7 2002; Hirata & Mizuno, 2011;), in which an individual will seize a heterospecific and interact
12 8 with it in a playful manner, sometimes killing it in the process. A leopard cub (*Panthera pardus*)
13 9 that was killed by adult chimpanzee males, was then carried like an infant for hours by a young
14 10 female (Hiraiwa-Hasegawa *et al.*, 1986). In wild bonobos, two cases were observed where young
15 11 males carried and interacted with live infant red-tailed monkeys which died, likely due to rough
16 12 handling. Following their death, the bonobos attempted to make the monkeys take hold of them
17 13 and one bonobo raised the monkeys’ arms and let them fall numerous times (Sabater-Pi *et al.*,
18 14 1993).

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21 15 While chimpanzees hunt a variety of animals, they only rarely scavenge on fresh
22 16 carcasses or feed on animals not killed in their presence by other chimpanzees (Watts, 2008;
23 17 Newton-Fisher, 2015). In fact, chimpanzees sometimes show apprehensive or fearful responses
24 18 towards dead heterospecifics (Goodall, 1986; Nishida, 1994). Muller *et al.* (1995) described
25 19 Gombe chimpanzees interacting with a dead adult bushbuck (*Tragelaphus scriptus*) – swatting
26 20 flies, poking, grooming, sniffing, ‘hoo’ calling, etc. – noting that only small pieces of flesh were
27 21 consumed, and solely by juveniles, with similar episodes witnessed at Ngogo (Watts, 2008).
28 22 Comparable responses have been observed to corpses of armadillos (*Oryzomys afer*) (Hosaka,
29 23 Inoue & Fujimoto, 2014) and bushpigs (*Potamochoerus larvatus*) or leopards (Nishida, 2012).
30 24 The classic field experiments of Kortlandt (1967) in wild chimpanzees revealed that they were
31 25 more fearful of dead and seemingly dead mammals or mammal models (mangabey, goat,
32 26 antelope) than when these were presented in lifelike postures. By contrast live animals were met
33 27 with little fear. In anubis baboons, experiments conducted at the Gilgil site, Kenya, show a
34 28 behavioural pattern possibly widespread among primates. When presented with gazelle
35 29 carcasses, baboons that had eaten from the carcass previously or observed others do so were
36 30 more likely to feed from it, whilst individuals with no prior contact with the carcass rejected it
37 31 (Strum, 1983).

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3 1 These observations suggest some resemblance between responses towards conspecifics
4 and non-conspecifics. This may be because corpses are not seen as potential prey (Boesch &
5 2 Boesch, 1989), generate an unusual/unfamiliar feeling that promotes fear or curiosity (Hosaka *et*
6 3 *al.*, 2014), or that a pathogen avoidance mechanism is involved (Watts, 2008) which would
7 4 explain why scavenging observations are rare. There is little/no consumption by chimpanzees of
8 5 corpses caught by leopards, a predator of chimpanzees (Muller *et al.*, 1995; Watts, 2008;
9 6 Nishida, 2012; Hosaka *et al.*, 2014), with recorded cases either representing assumptions or
10 7 confounded by human interaction (Hasegawa *et al.*, 1983).
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19 **IV. PRIMATE THANATOLOGY: EVOLUTIONARY/COGNITIVE ASPECTS**

20 **(1) A naïve theory of life**

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22 12 Primates divide their world into agents and non-agents. Agents are living entities capable
23 13 of engaging in self-generated motion, exhibiting goal-directedness and contingency, and acting
24 14 upon and reacting to objects, events and other agents in their world (Barrett, 2005; Spelke &
25 15 Kinzler, 2007; Carey, 2009). This conserved perceptual-cognitive feature conveys a critical
26 16 advantage in predator–prey detection. In a visual world, many animals have evolved ways to
27 17 conceal themselves *via* mimicry or colour change (Stevens & Merilaita, 2009), or engage in
28 18 behaviours such as freezing (Hagenaars, Oitzl, & Roelofs, 2014) or thanatosis (Humphreys &
29 19 Ruxton, 2018).
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36 20 In primates, life detection is one of many Core Knowledge Systems, in this case, the Core
37 21 System of Agency (CSA), for which there is evidence for a dedicated neural pathway in
38 22 macaques (Sliwa & Freiwald, 2017). Core Knowledge Theory proposes that hard-wired
39 23 cognitive skills shape mental representations about the world (Carey, 2009). Using Leslie's
40 24 (1994) tripartite division of agency as a starting point, we outline how life is perceived in primate
41 25 brains at three levels of agency:
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46 26 (1) *Animate agency* – this level pertains to the animacy detection system and is governed
47 27 by two dimensions: shape and movement. These perceptual cues arise in the form of mechanisms
48 28 such as biological motion perception, a gaze detection module, and a face detection module,
49 29 comprising components partly of innate character and partly acquired during ontogeny.
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53 30 Detecting eyes looking directly at the observer conveys information critical for survival;
54 31 computations such as this in predator–prey interactions have been termed ‘the beginnings of
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1 mind-reading' (Barrett, 2015). The existence of an eye-direction detector (EDD) or gaze
2 detection module was proposed by Baron-Cohen (1995) as a specialised neural system that
3 functions by sensing eyes and eye-like stimuli in the environment. In the primate social sphere,
4 attending to eyes can arbitrate both affiliative and aggressive interactions (Emery, 2000), and its
5 effectiveness as a stimulus has been shown in the cognition literature (Batki *et al.*, 2000;
6 Myowa-Yamakoshi & Tomonaga, 2001; Myowa-Yamakoshi *et al.*, 2003; Farroni, Johnson &
7 Csibra, 2004). From birth, primates engage in face-to-face exchanges.

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

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

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

29 For perspective taking, there seems to be a difference between Old and New World
30 primates. In hidden food experiments, using the conspecific competition paradigm, capuchin
31 monkeys (Hare *et al.*, 2003) and common marmosets (Burkart & Heschl, 2007), unlike

1 chimpanzees (Hare *et al.*, 2000; Hare, Call & Tomasello, 2001) and rhesus macaques
2 (Flombaum & Santos, 2005), consistently fail to reason about what the competitor can and
3 cannot see. Such abilities appear to require a more mentalistic kind of agency.

4 (3) *Mentalistic agency* – researchers have long endeavoured to uncover a theory of mind
5 (inferring the mental states of others) in non-human animals (reviewed in Call & Tomasello,
6 2008). Monkeys appear unable to do this (Martin & Santos, 2014), with sensitivity to the
7 existence of rivals and their gaze path as simpler explanations than connecting the act of seeing
8 to knowing (MacLean & Hare, 2012). One suggested mental device that uses mind-reading
9 abilities is experience projection, which has been demonstrated in chimpanzees (Karg *et al.*,
10 2015). It was proposed that chimpanzees might possess a minimal theory of mind with false-
11 belief attribution being a limiting boundary of their mindreading capabilities (Call & Tomasello,
12 2008); however, recent studies (Krupenye *et al.*, 2016; Buttelmann *et al.*, 2017) have revealed
13 that great apes do possess implicit knowledge of false-beliefs – a fundamental aspect of the
14 theory of mind.

16 (2) Levels of death awareness

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

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

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

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

8 We know that monkeys recognise that a solid object cannot pass through another solid
9 object (Santos & Hauser, 2002) or move unless contacted by another moving object (Hauser,
10 1998). When seeing a human reaching for an object, five and seven-month-old infants react to
11 changes in their goals (Woodward, 1998); no such response is observed when a rod/claw reaches
12 for the same object (Woodward, Somemerville & Guajardo, 2001; Hofer, Hauf & Aschersteben,
13 2005; Daum & Gredebäck, 2011) unless replaced by a realistic humanoid robot (Kamewari *et*
14 *al.*, 2005; also see Arita *et al.*, 2005). Similar results have been found in capuchin monkeys
15 (*Sapajus apella*) (Phillips *et al.*, 2009), whilst in common marmosets the use of a monkey-like
16 robot, but not a moving box, induces goal-direction ascription (Kupferberg, Glasauer & Burkart,
17 2013). While human infants (of nine, 10 and 18 months) tend to imitate the goal-directedness of
18 a human actor, they do not readily imitate analogous actions of a mechanical actor (Meltzoff,
19 1995; Legerstee & Markova, 2008, Boyer, Pan & Bertenthal, 2011). Infants (of 12 weeks and
20 two months) show differences in looking time when presented with a human *versus* a toy
21 monkey, and smile and coo only with the former (Brazelton, Koslowski & Main, 1974;
22 Trevarthen, 1977). Seven-month-olds appreciate that humans, but not objects, can exhibit self-
23 propelled motion (Spelke, Phillips & Woodward, 1995; Markson & Spelke 2006), and nine-
24 month-olds become distressed upon seeing inanimates moving on their own (Poulin-Dubois,
25 Lepage & Ferland, 1996). Even to the naïve brain, movement by itself is not a sufficient
26 condition for agency – a rule that makes sense for all species, since, while the natural world can
27 produce animate movement in inanimates, it does so in a predictable fashion (i.e. rivers, falling
28 leaves, rain). Only upon encountering agents or entities with agent-like properties is the CSA
29 activated.

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

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

14 These brain areas are also critical for learning processes. Clearly, death is a common
15 occurrence in the animal kingdom. It has been claimed that primates might be able to distinguish
16 between the presence and absence of agency (Anderson, 2011), making it conceivable that group
17 members that have witnessed such events before can gather both contextual and sensory
18 information to be retrieved on similar occasions (Gonçalves & Biro, 2018). Notably, since
19 primates live in social environments, there are abundant opportunities for them to interact with
20 dead conspecifics, acquaint themselves with death cues and integrate them in a limited sense (i.e.
21 a dead individual that once afforded movement and sound is gradually re-categorised as one that
22 does neither). Observations on monkeys suggest that this re-categorisation is rather fluid. Booth
23 (1962) notes that captive vervet monkeys (*Chlorocebus aethiops*) sometimes abandon sickly
24 infants too weak to move and appearing dead. Moreover, she observed that if stillborns are
25 accidentally pushed by the mother resulting in short-term movement or if a human observer
26 deliberately pushes it making it appear to be self-propelled, the mother's attention is instantly
27 activated, stimulating her to lick it in an agitated fashion. Correspondingly, and contrary to a
28 non-responsive infant, a moving stuffed natal coat carried by a human triggers rescue attempts
29 from the group, which subside as soon as the infant skin is left motionless (see also *post-mortem*
30 spasms; Anderson *et al.*, 2010; Pruetz *et al.*, 2017).

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3 1 Finally, since the corpse of a conspecific may evidence a predation event and
4
5 2 consequently critical danger, natural selection might have acted on developmental systems that
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7 3 promote rapid acquisition of such knowledge through associative learning mechanisms *via* social
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9 4 knowledge – basic phenomena shared by many animals but separate from notions of death as a
10
11 5 universal and permanent state.

12 6 (3) *Death awareness* – dead is not the same thing as death (Kastenbaum, 2000): dead (the
13
14 7 state) is the physical result of the phenomenon of death (the event). Awareness of death has been
15
16 8 a considerable object of study in developmental psychology (Speece & Brent, 1996; Slaughter,
17
18 9 Jaakkola & Carey, 1999; Kenyon, 2001). Research on the concept of death in humans, generally
19
20 10 in the form of structured interviews, suggests that children acquire separate subcomponents of
21
22 11 death at distinct periods in development (see Table 2).

23 12 Many factors are involved in the acquisition of a mature concept of death such as age,
24
25 13 cognitive development, and previous experience (Hunter & Smith, 2008). Evidence shows that
26
27 14 children grasp the physical aspects of Cessation (body stops functioning) and understand its
28
29 15 psychological aspects (dead cannot think nor dream) (Bering, McLeod & Shakelford, 2005).
30
31 16 Likewise for Causation, younger children realise that external factors (accidents, predation, etc.),
32
33 17 cause death before they comprehend that internal factors (breakdown of bodily functions)
34
35 18 contribute to it. Without this ‘scientific’ aspect of Causation (Kenyon, 2001) a mature concept of
36
37 19 death would be acquired at earlier ages. Experience with death appears to accelerate death-
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39 20 concept acquisition; children with direct death experience show a more mature understanding of
40
41 21 death *versus* inexperienced age-mates (Kenyon, 2001; Hunter & Smith 2008; Bonoti, Leondari &
42
43 22 Mastora, 2013). Same-age groups tend to show similar understanding regarding animal death,
44
45 23 again likely due to previous experience (Orbach *et al.*, 1987; Bonoti *et al.*, 2013). Studies using
46
47 24 realistic stimuli (photographs or stuffed animals) found that three year olds performed
48
49 25 significantly better in discriminating living *versus* dead states than conventional studies (i.e.
50
51 26 interviews) show [Behrend (1984) and Sprent *et al.* (1996) both cited in Barrett & Behne, 2005].
52
53 27 Indeed, exposure to corpses remains a powerful source of knowledge of death for young children
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55 28 (Astuti, 2011). As they attain a concept of death, children seemingly rely on inductive and
56
57 29 analogical reasoning to achieve and revise it by extending human qualities/experiences to other
58
59 30 scenarios including living beings (Carey, 1985; Slaughter, 2005).
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3 1 One standout study is that of Barrett & Behne (2005). Contradicting previous claims,
4 2 they argued for a death detection mechanism, which functions as a subroutine of the CSA (or
5 3 agency detection system) that switches off agency inferences when reliable cues to death are
6 4 available. To test their cessation of agency hypothesis, they interviewed two populations of
7 5 children from different cultural backgrounds on sleep *versus* death conditions, and found that
8 6 children as young as four already show a clear understanding of death with regards to Causation
9 7 and Cessation, suggesting a strong mechanism regardless of personal and cultural differences
10 8 (Barrett & Behne, 2005; Barrett, 2005).

11 9 Their cessation of agency hypothesis (Barrett & Behne, 2005; Barrett, 2005) makes a few
12 10 important claims about death inferences in an evolutionary framework. In ancestral
13 11 environments, members of the *Homo* lineage would have encountered a variety of living animals
14 12 which they were already naturally selected to monitor as possible sources of danger (see Section
15 13 III.1). Through frequent interaction with dead animals, including potential sources of food,
16 14 reliable cues to and/or knowledge of the cause of death would activate a 'switch' or an
17 15 expectancy shift (Kastenbaum, 2000) promoting a re-categorisation from living to dead. Not
18 16 being able to make such a distinction would be energetically costly since it unnecessarily
19 17 prolongs alert states (Dukas & Clark, 1995).

20 18 At Tāi Forest, Boesch (2012) observed chimpanzees displaying more fearful reactions to
21 19 dead individuals that died of disease than to individuals that died from leopard predation (10
22 20 cases *versus* 5 cases, respectively). Moreover, they tended to lick wounds of injured
23 21 conspecifics, something they never did with dead ones. These distinctions seemed to rely on an
24 22 understanding of death when reliable cues were available and appear to indicate chimpanzees
25 23 have an implicit awareness of death; living individuals have their wounds tended, dead ones do
26 24 not, and unexplainable deaths (no visible wounds) rather than explainable ones (visible wounds)
27 25 induce the most fear. Taken together these reports imply that chimpanzees may have a limited
28 26 capacity for the subcomponents of Causality and Irreversibility.

29 27 Irreversibility can also be assessed through violation of expectations: when a dead
30 28 individual is confidently re-categorised as dead, seeing it alive again can elicit a strong emotional
31 29 response. An anecdote by de Waal (2001) illustrates such a scenario in captive chimpanzees. In
32 30 the Arnhem Zoo, a documentary had been produced depicting its chimpanzee population. During
33 31 its development one male Nikkie, had died. When the documentary was projected to them and

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2
3 1 when the dead chimpanzee appeared on screen the two remaining males had a fearful reaction:
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5 2 “It remains unclear whether the apes recognized the actors, until a life-sized Nikkie appeared. At
6
7 3 that point Dandy immediately ran screaming to Yeroen, jumping literally in the old male’s lap!
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9 4 Yeroen, too, had an uncertain grin on his face. Nikkie’s mysterious resurrection had temporarily
10
11 5 restored their old pact.” (de Waal, 2001, p. 305).

12 6 Kordlandt (1967, p. 204) observed fearful responses in wild chimpanzees to
13
14 7 experimentally placed dead or dead-like mammals in contrast to living ones, and concluded that
15
16 8 “chimpanzees have some kind of notion what life and death are, (...) however vague this notion
17
18 9 might be”. Bering (2001) argued that chimpanzees possess an awareness of biological death,
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20 10 meaning, like three-year-old humans, that they appreciate changes in state, but do not possess an
21
22 11 awareness of psychological death (the end of cognitive functions). Other researchers have made
23
24 12 bolder claims. Gallup (1979, 1998), through his mirror self-recognition experiments on great
25
26 13 apes, suggested that with self-awareness comes an awareness of one’s own mortality. Premack
27
28 14 (1976) raised the possibility of teaching a chimpanzee about its own future death, but dismissed
29
30 15 it on ethical grounds, while ASL studies on great apes remain inconclusive (Patterson & Gordon,
31
32 16 1993; Fouts & Mills 1997). Likewise, de Waal, stated that “Seeing the termination of a familiar
33
34 17 individual’s life, chimpanzees may respond emotionally as if realising, however vaguely, what
35
36 18 death means” (de Waal, 1996, p. 56), and that “might these individuals not apply what they have
37
38 19 learned about life and death to their own bodies? It’s hard to know, yet impossible to rule out.”
39
40 20 (de Waal, 2013, p. 210). Such ability would likely require a capacity for the animal to mentally
41
42 21 project itself into the future, and there is convincing evidence that great apes can do this in other
43
44 22 contexts (reviewed in Osvath, 2016).

45 23 The rather persuasive examples of non-human primate awareness of death mainly include
46
47 24 the great apes. In comparison to monkeys, great apes perform better at cognitive tasks requiring
48
49 25 the use of analogical reasoning, future-oriented reasoning and mirror self-recognition, with
50
51 26 monkeys usually needing extensive training to succeed at such tasks (reviewed in Vonk, 2003;
52
53 27 Osvath & Persson, 2013; Anderson & Gallup, 2015; Thompson, Flemming & Hagemann, 2016).
54
55 28 Taken together, they suggest that these cognitive abilities are not as normative in monkeys as
56
57 29 they appear to be in great apes. Many of these abilities are related to executive functions, high-
58
59 30 level cognitive processes that optimise behaviour, believed to emerge mainly in the prefrontal
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31 cortex (i.e. emotional regulation, inhibitory control, working memory and forethought). The

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2
3 1 prefrontal cortex underwent considerable expansion during ape evolution – a trend beginning in
4 2 the Miocene 19–15 million years ago (mya) and continued in the genus *Homo* (Smaers *et al.*,
5 3 2017). As a whole, these studies along with captive and wild thanatological reports place great
6 4 apes as the likeliest candidates for achieving aspects of a human-like concept of death (i.e.
7 5 irreversibility, causation), nonetheless the burden of proof still awaits future research.

8
9
10 In conclusion, primates and other socially complex animals, *via* their sensory modalities
11 6 and cognitive and learning processes, can distinguish dead from live states (Gonçalves & Biro,
12 7 2018) (Fig. 8). However, the claim that primates may have more than an implicit awareness of
13 8 death currently stands on *terra incognita*; the available evidence, while highly suggestive, is not
14 9 yet the most compelling.
15 10
16 11

12 (3) Grief becomes mourning

13 Conjectures have been made regarding the thanatological behaviour of extinct primates.
14 13 Pettitt (2011), assessing data from chimpanzees, suggested that such behaviours might reach as
15 14 far back as the Miocene apes 23–5 mya. Given that the fossil record for anthropoids emerges
16 15 some 45 mya (Beard, 2016), and that dead-infant carrying is prevalent among extant monkeys
17 16 and apes, it is likely that this practice was present throughout the Eocene and well into the
18 17 Pleistocene, with all the behavioural features that accompany it. The living primate species that
19 18 engage most often in dead-infant carrying behaviour are typically terrestrial and/or capable of
20 19 bipedal carriage, implying that hominin lineages with brain capacities and structure comparable
21 20 to chimpanzees, such as ardipithecines and australopithecines (Suwa *et al.*, 2009), may have
22 21 carried their dead infants and exhibited a similar thanatological repertoire to extant great apes.

23 During human evolution, such behaviours gradually gave way to more ritualised
24 23 mortuary activities, including burial practices and beliefs in the afterlife (Stiner, 2017). This
25 24 transition has not been thoroughly placed in an evolutionary framework, with three noteworthy
26 25 exceptions from the fields of archaeology (Pettitt, 2011), philosophy (Sheets-Johnstone, 1986),
27 26 and primatology (Anderson, 2017). Pettitt (2011) outlined five stages of mortuary behaviour
28 27 development: core mortuary, archaic mortuary, modernising mortuary, modern mortuary, and
29 28 advanced mortuary. The behaviours described herein constitute the core mortuary phase, present
30 29 in apes and anthropoid monkeys, with the corpse invariably being relinquished *in situ*. The later
31 30 stages of mortuary behaviour are characterised by the mode in which the corpse is left; structured

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3 1 abandonment (deliberate deposition of the corpse in a given place) and funerary caching
4 (placement of the corpse in pits, caves or natural fissures) occur in the archaic mortuary phase,
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6 3 whilst cairn covering (stones covering the corpse) and inhumation occur as part of the
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8 4 modernising mortuary phase. Boesch (2012) observed chimpanzee corpses at Tâi forest being
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10 5 covered with leafy branches by conspecifics. However, similar to the evolution of nest building
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12 6 in great apes (Sept, 1998), it remains challenging to determine whether comparable behaviours
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14 7 occurred in hominins due to the perishable nature of such materials. Nonetheless, this could
15
16 8 account for the large gaps in the mortuary record during the archaic mortuary phase.

17 9 Despite being matters of contention, there are archaeological sites that may fill the
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19 10 mortuary gaps in the Palaeolithic period. Pettitt (2011) interprets the AL-333 fossil site as an
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21 11 example of structured abandonment, containing the corpses of some 13 individuals of
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23 12 *Australopithecus afarensis* that were presumably placed in a field amidst tall grass by their
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25 13 conspecifics around 3–3.5 mya. The earliest probable examples of funerary caching were
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27 14 practiced by *Homo heidelbergensis* around 350–450 thousand years ago (kya) (Carbonell &
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29 15 Mosquera, 2006; Sala *et al.*, 2016) and *Homo naledi* at 236–335 kya (Dirks *et al.*, 2015; Berger
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31 16 *et al.*, 2017), with *Homo neanderthalensis* and *Homo sapiens* burials overlapping from 80–34
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33 17 kya (Pettitt, 2015).

34 18 What do mortuary and funerary rituals signal and what purpose do they serve? In the case
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36 19 of Palaeolithic burials, the underlying motivations appear to be of compassionate nature rather
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38 20 than practical disposal. An observable trait of earlier hominins is their high degree of
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40 21 compassion, where group members took care of their sick and injured, delaying their demise
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42 22 (reviewed in Hublin, 2009). Stiner (2017) makes important claims regarding this. First, most of
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44 23 these burials occur in residential campsites within or near social sites significant to the living.
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46 24 Second, since the assortment of animal carcasses and organic remains often found scattered in
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48 25 camps would have contributed to strong smells, burying a group member to remove the offensive
49
50 26 stench seems unlikely. Third, considering these were nomadic groups, moving camp rather than
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52 27 cleaning up and leaving the bodies along with other animal remains would have required less
53
54 28 effort. Finally, rather than burying a corpse so as not to attract potential scavengers (Boyer,
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56 29 2001) our ancestors might have been simply displaying care for the deceased by protecting them
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58 30 from scavengers.
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3 1 Rossano (2015) argues that the elaborate burials seen in the Upper Paleolithic have a
4 2 ritualistic component indicating behavioural cost in terms of time, effort and resources, all of
5 3 which evidence credible displays of social commitment. However, short of relinquishing the
6 4 corpse *in situ*, any mortuary treatment will involve a cost regardless of ritual components.
7 5 Deliberate placing of corpses in a specific open areas (structured abandonment) or natural
8 6 fissures or caves (funerary caching) involves moving them to such places. They must have been
9 7 carried/dragged by either one individual which is energetically demanding and suggests close
10 8 emotional bonds or, perhaps, as a group effort which, albeit less demanding, undeniably
11 9 indicates shared intentionality. Shared intentionality (i.e. the ability to share attention and
12 10 emotional/cognitive states and coordinate actions grounded in these states) is described as a
13 11 foundational human behavioural feature (Tomasello & Carpenter, 2007). At a basic level, these
14 12 practices show that earlier hominins appreciated that death was a different state and thus corpses
15 13 required particular treatment.

16 14 Noting the extensive exposure to death cues through visual and physical contact directed
17 15 at corpses across human cultures, White, Marin & Fessler (2017) propose that mourning rituals
18 16 serve an evolutionarily selected purpose. The death of a group member may not only be
19 17 detrimental to immediate family by decreasing inclusive fitness but would also impact the wider
20 18 group. Functionally speaking, mourning ceremonies shorten the grieving process by allowing
21 19 ritualised re-categorisation from living to dead and facilitate the restructuring of social bonds
22 20 through replacement. Moreover, in modern humans, mothers that hold their dead stillborn report
23 21 fewer anxiety and depressive symptoms in comparison to mothers that do not (Cacciatore,
24 22 Rådestad & Frøen, 2008) suggesting a grief-management component to such practices.

25 23 Extant primates, due to ecological and evolutionary constraints (i.e. foraging lifestyle),
26 24 typically abandon injured/sick individuals. That is not to say they show no empathy or concern in
27 25 the contexts of death, injury and disease (see Boesch *et al.*, 2010, Pruett, 2011; Tokuyama *et al.*,
28 26 2012; Bezerra *et al.*, 2014), rather their treatment of such individuals is mostly confined to the
29 27 mother–infant bond (Turner, Gould & Duffus, 2005; Matsumoto *et al.*, 2016). Abandonment of
30 28 ill/fatally injured individuals is the culmination of what is often a protracted surrender of such
31 29 individuals by their group (van Lawick-Goodall, 1971; Fossey, 1983; Goodall, 1986; Strum,
32 30 1987; Yang *et al.*, 2016). However, their failure to engage in the more elaborate mortuary
33 31 behaviours exhibited by early hominins indicates a cognitive disparity between human and non-

1 human primates. Since the panini (chimpanzees and bonobos) and hominini lineages diverged
2 some 5–7 mya, the latter underwent significant physical and behavioural innovations. Biological
3 trends included bipedal specialisations and increased brain size (from the 400 cm³ of
4 Australopithecines to the roughly 1400 cm³ of *Homo sapiens*) but also cortical re-organisation
5 (increased dominance of the prefrontal regions) (Holloway, 2015). Behavioural advances
6 included a flaked stone industry with increased technological complexity over time (Toth &
7 Schick, 2018), emergence of language (Morgan *et al.*, 2015), control of fire as early as 1mya
8 (Berna *et al.*, 2012) and the appearance of the funeral rituals discussed above. Together, these
9 examples illustrate a growth in intellect and prosociality in our lineage with levels far exceeding
10 those observed in primates today.

11 12 **(4) General findings and future directions**

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

29 Loss of a social partner can negatively impact fitness in the living and promote a shift in
30 the hierarchical order. Assuming that primates can extract valuable albeit limited information
31 from dead conspecifics (*sensu* Cronin *et al.*, 2011; White *et al.*, 2017), there are indirect

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3 1 evolutionary benefits to thanatological responses. In the context of a social group, we suggest
4 interactions with the dead: (1) promote more rapid re-categorisation from living to dead; (2)
5 decrease costly vigilance/caregiving behaviours; (3) are crucial to the management of grieving
6 responses; (4) update individual position in the group hierarchy; and (5) accelerate the formation
7 of new social bonds.
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12 6 Acquisition of an advanced concept of death (with the subcomponents of Universality,
13 Irreversibility, Cessation and Causation) developed during human evolution through the
14 expansion of the neocortex. This allowed abilities to develop such as high-order reasoning,
15 essential to an understanding of death as suggested by archaeological evidence on mortuary
16 practices among our ancestors in the genus *Homo* and the developmental/cognitive literature in
17 humans.
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23 12 Primate thanatology has recently benefitted from careful ethological observations which
24 could be complemented by hormonal measurements (Engh *et al.*, 2006; Kaplan *et al.*, 2012)
25 carried out in a systematic fashion. Social Network Analysis could provide a useful tool to
26 analyse the social impact on a group of the death of one of its members (*sensu* Kanngiesser *et al.*,
27 2011). Relating to the claim that wild chimpanzees do not tend wounds of the dead (Boesch,
28 2012), we do not know if this also applies to other less cognitively complex primate species
29 known to tend wounds in the living. We also know very little about the occurrence of visitations
30 to a corpse, since primate groups can be difficult to track; the use of camera-traps strategically
31 positioned near a corpse could uncover the frequency of such interactions. A data-collection
32 protocol should include an ethogram detailing primary and secondary interactions (see Appendix
33 S1–S4), describe the social and kin relationships and, particularly in case of dead-infant carrying,
34 the cause of death, observation date, temperature/humidity, and parity and rank of the mother.
35 Such data could be included in an online database to facilitate future comparisons.
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45 25 There have also been many experimental paradigms that inform on how primates respond
46 to dead individuals. Barrett & Behne (2005) suggest that disruptions of the body envelope could
47 provide an important cue for death. Earlier applications and indirect evidence of this can be
48 found in Hebb (1946) and Butler (1964). Since such responses occur in a violation-of-
49 expectation scenario, using a looking-time paradigm in such experiments could prove effective.
50 This could be achieved using video recordings and eye-tracking technology to challenge
51 expectations of Causality and Irreversibility (i.e. simulated killing of a conspecific and it
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3 1 returning to life). Another method would be to play back calls of a recently deceased individual
4 2 to members of its group (*sensu* Allen & Hauser, 1991; Palombit *et al.*, 1997), for instance,
5 3 bonobos can recognise recordings of a social partner even after years of separation (Keenan *et*
6 4 *al.*, 2016). Touch-screen matching-to-sample tasks depicting death and life as natural categories
7 5 could demonstrate whether primates show any generalisation from subordinate to basic and
8 6 superordinate category levels (i.e. dead conspecific to dead animal to decayed organic matter,
9 7 respectively). Besides visual and audio modalities, olfaction could also play a role in determining
10 8 these responses (Sarabian & MacIntosh, 2016; Wisman & Shrira, 2015) through scent and visual
11 9 matching (i.e. rotten smell with dead animal picture). Given that the Animate/Inanimate
12 10 distinction arises in different areas of the brain, it is unclear how corpses are represented. Neuro-
13 11 imaging studies could provide insights into how primates process living and non-living entities
14 12 (*sensu* Cross *et al.*, 2013). Experimental methodologies should, of course, be devised to avoid
15 13 distress or lasting harm to the animals (Prescott, 2010)

16 14 Many areas of inquiry remain, and whilst ethological reports are informative, resumption
17 15 of experimental research methodologies confined within the ethical boundaries of animal
18 16 research will be critical to advance the emerging field of primate thanatology.

19 17

20 18 **V. CONCLUSIONS**

21 19 (1) Based on literature surveyed from the 19th century onwards, primates have long been
22 20 observed performing thanatological behaviours, corroborated by independent present-day
23 21 observations, such as grieving, carrying the dead, and protecting the body.

24 22 (2) Dead-infant carrying behaviour appears to represent part of a continuum of caretaking
25 23 behaviours upon which natural selection has acted in the mammalian lineage. Such behaviours
26 24 occur independent of the cause of death, although contextual and sensory cues to death might
27 25 impact their duration. Whilst strepsirrhines and callitrichines do not engage in these behaviours,
28 26 possibly due to postural/anatomical and behavioural constraints, the affective behaviours they
29 27 exhibit towards their deceased infants are similar to other mammalian species.

30 28 (3) Dead adult and juvenile individuals engender greater attention from the group in comparison
31 29 to dead infants. This not only depends on sex, rank and kinship of the dead individual but also on
32 30 the social organisation of the group (multi-male/multi-female groups *versus* uni-male/multi-
33 31 female groups).

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3 1 (4) Behaviour towards dead group members includes direct interactions (hit, pull, groom, etc.).
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5 2 Depending on the context, some of these actions give the impression of attempts to rouse the
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7 3 corpse, while others may be attempts to monopolise the corpse or attacks on the dead
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9 4 individual's perceived failure to comply submissively to displays. Guarding the body, vigils,
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11 5 visitations, avoidance of the place of death and abandonment are among the typical behavioural
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13 6 features exhibited by primates.

14 7 (5) Vocalisations emitted during these interactions are usually alarm calls, distress cries and
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16 8 cohesion-related communication that signal both the internal emotional state and a danger
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18 9 assessment. The corpse of a conspecific triggers a set of behaviours consistent with a scenario of
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20 10 novelty/danger and violation-of-expectation whereupon a previously known group member
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22 11 ceases its agency.

23 12 (6) Primates appear to have an implicit awareness of death wherein the dead individual ceases its
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25 13 agency. Some observations suggest that they may be capable of Irreversibility and Causation. As
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27 14 a concept however, it is incomplete as individuals require frequent updates on the status of the
28
29 15 dead (i.e. guarding, vigils, visitations). This could reflect attachment towards the dead
30
31 16 conspecific confounding such awareness, as other individuals may cease rapidly to treat the
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33 17 individual as if it were alive.

34 18 (7) Our integrated model of life-death awareness proposes that primates are capable of at least
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36 19 two levels of death awareness. The first level is governed by perceptual categorisation, whilst the
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38 20 second is governed by associative concepts. A third level is governed by high-order reasoning
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40 21 (analogical/inductive/causal reasoning). Species possessing all these cognitive traits are in a
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42 22 likely position to acquire an emergent conceptual awareness of death similar to humans. Present
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44 23 cognitive research suggests that, among the primates, the great apes are the best candidates for
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46 24 such a position.

47 25 (8) Given their occurrence throughout the primate order, thanatological behaviours were likely to
48
49 26 have been present in human ancestors from the Eocene through to the Pleistocene (45–3 mya).
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51 27 These examples of core mortuary behaviour would have persisted alongside emerging instances
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53 28 of archaic mortuary practices in the form of structured abandonment and funerary caching (3
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55 29 mya–235 ka), culminating in the development of mortuary rituals such as formal burials (80–35
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57 30 ka). The elaboration in thanatological behaviour during hominin evolution was accompanied by
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3 1 cortical expansion and reorganisation as expressed in tool-making, control of fire and the
4 emergence of language.
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6 3 (9) Although thanatological interactions imply attachment relationships and could operate on the
7 expectation the dead individual could recover, they may serve an evolutionary purpose by
8 gathering information on the conspecific's state. Their additional role would be to promote a
9 more rapid re-categorisation from living to dead, reduce costly vigilant/caregiving behaviours, be
10 essential to the management of grieving responses, update ranks in the group's hierarchy, and
11 accelerate the formation of new social bonds.
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33 VII. REFERENCES

- 34
35 19 AGORAMOORTHY, G. & HSU, M. J. (2005). Occurrence of infanticide among wild proboscis
36 20 monkeys (*Nasalis larvatus*) in Sabah, Northern Borneo. *Folia Primatologica* **76**, 177–179.
37 21
38 22 AGORAMOORTHY, G. & MOHNOT, S. M. (1988). Infanticide and juvenicide in Hanuman langurs
39 23 (*Presbytis entellus*) around Jodhpur, India. *Human Evolution* **3**, 279–296.
40 24
41 25 AGORAMOORTHY, G. & RUDRAN, R. (1995). Infanticide by adult and subadult males in free-
42 26 ranging red howler monkeys, *Alouatta seniculus*, in Venezuela. *Ethology* **99**, 75–88.
43 27
44 28 ALFRED, J. R. B. & SATI, J. P. (1991). On the first record of infanticide in the hoolock gibbon -
45 29 *Hylobates hoolock* in the wild. *Records of the Zoological Survey of India* **89**, 319–321.
46 30
47 31 ALLEN, C. & HAUSER, M.D. (1991). Concept attribution in nonhuman animals: theoretical and
48 32 methodological problems in ascribing complex mental processes. *Philosophy of Science* **58**, 221–
49 33 240.
50 34
51 35 ALLEY, T. R. (1980). Infantile colouration as an elicitor of caretaking behaviour in old world
52 36 primates. *Primates* **21**, 416–429.
53 37
54
55
56
57
58
59
60

- 1
2
3 1 ALTMANN, J. (1980). *Baboon mothers and infants*. Harvard University Press, Cambridge M.A.
4 2
5 3 ALVAREZ, S., DI FIORE, A., CHAMPION, J., PAVELKA, M. S., PÁEZ, J. & LINK, A. (2015). Male-
6 4 directed infanticide in spider monkeys (*Ateles* spp.). *Primates* **56**, 173–181.
7 5
8 6 ANDERSON, J. R. (1984). Ethology and ecology of sleep in monkeys and apes. *Advances in the*
9 7 *Study of Behavior* **14**, 165–229.
10 8
11 9 ANDERSON, J. R. (2011). A primatological perspective on death. *American Journal of*
12 10 *Primatology* **73**, 410–414.
13 11
14 12 ANDERSON, J. R. (2016). Comparative thanatology. *Current Biology* **26**, R553–R56.
15 13
16 14 ANDERSON, J. R. (2017). Comparative Evolutionary Thanatology of Grief, with Special
17 15 Reference to Nonhuman Primates. *Japanese Review of Cultural Anthropology* **18**, 173–189.
18 16
19 17 ANDERSON, J. R. & GALLUP, G. G. (2015). Mirror self-recognition: a review and critique of
20 18 attempts to promote and engineer self-recognition in primates. *Primates* **56**, 317–326.
21 19
22 20 ANDERSON, J. R., GILLIES, A. & LOCK, L. C. (2010). Pan thanatology. *Current Biology* **20**,
23 21 R349–R351.
24 22
25 23 ARCHER J. (1999). *The nature of grief: the evolution and psychology of reactions to loss*.
26 24 Routledge, London.
27 25
28 26 ARITA, A., HIRAKI, K., KANDA, T. & ISHIGURO, H. (2005). Can we talk to robots? Ten-month-
29 27 old infants expected interactive humanoid robots to be talked to by persons. *Cognition* **95**, B49–
30 28 B57.
31 29
32 30 ASCHEMEIER, C. R. (1921). On the gorilla and the chimpanzee. *Journal of Mammalogy* **2**, 90–92.
33 31
34 32 ASTUTI R. (2011). Death, ancestors, and the living dead: learning without teaching in
35 33 Madagascar. In *Children's understanding of death: from biological to supernatural conceptions*.
36 34 (eds V. TALWAR, P. L. HARRIS and M. SCHLEIFER), pp. 1–18. Cambridge University Press, New
37 35 York.
38 36
39 37 AVERILL, J. R. (1968). Grief: its nature and significance. *Psychological Bulletin* **70**, 721–748.
40 38
41 39 BALASUBRAMANIAN, M. & SABU-JAHAS, S. A. (1997). An observation on a mother carrying
42 40 dead infant in the bonnet macaque, *Macaca radiata*. *Journal of the Bombay Natural History*
43 41 *Society* **94**, 143–143.
44 42
45 43 BALDERSTON, N. L., SCHULTZ, D. H. & HELMSTETTER, F. J. (2013). The effect of threat on
46 44 novelty evoked amygdala responses. *PloS one* **8**, e63220.
47 45
48 46 BARATAY, E. & HARDOUIN-FUGIER, E. (2003). *Zoo: A history of zoological gardens in the West*.
49 50
50 51
51 52
52 53
53 54
54 55
55 56
56 57
57 58
58 59
59 60
60

- 1
2
3 1 Reaktion Books Ltd, London.
4 2
5 3 BARON-COHEN, S. (1995). The eye direction detector (EDD) and the shared attention mechanism
6 4 (SAM): Two cases for evolutionary psychology. In *Joint attention: Its origins and role in*
7 5 *development*. C. MOORE & P. J. DUNHAM (Eds.), pp. 41–59. Hillsdale, NJ, US: Lawrence
8 6 Erlbaum Associates, Inc
9 7
10 8 BARRETT H. C. (2005). Adaptations to predators and prey. In: *The handbook of evolutionary*
11 9 *psychology*. (ed D. M. BUSS), pp. 200–223. Wiley, New York.
12 10
13 11 BARRETT, H. C. (2015). *The shape of thought: How mental adaptations evolve*. Oxford
14 12 University Press, New York.
15 13
16 14 BARRETT, H. C. & BEHNE, T. (2005). Children's understanding of death as the cessation of
17 15 agency: a test using sleep versus death. *Cognition* **96**, 93–108.
18 16
19 17 BARRETT, L. (2012). Why behaviorism isn't satanism. In *The Oxford handbook of comparative*
20 18 *evolutionary psychology*. (eds J. VONK and T. K. SHACKELFORD), pp. 17–38. Oxford University
21 19 Press Inc, New York.
22 20
23 21 BATKI, A., BARON-COHEN, S., WHEELWRIGHT, S., CONNELLAN, J. & AHLUWALIA, J. (2000). Is
24 22 there an innate gaze module? Evidence from human neonates. *Infant Behavior and Development*
25 23 **23**, 223–229.
26 24
27 25 BEARD, K. C. (2016). Out of Asia: anthropoid origins and the colonization of Africa. *Annual*
28 26 *Review of Anthropology* **45**, 199–213.
29 27
30 28 BEKOFF, M. (2010). *The emotional lives of animals: A leading scientist explores animal joy,*
31 29 *sorrow, and empathy—and why they matter*. New World Library, Novato.
32 30
33 31 BELL, A. H., HADJ-BOUZIANE, F., FRIHAUF, J. B., TOOTELL, R. B. & UNGERLEIDER, L. G.
34 32 (2009). Object representations in the temporal cortex of monkeys and humans as revealed by
35 33 functional magnetic resonance imaging. *Journal of Neurophysiology* **101**, 688–700.
36 34
37 35 BELTRÁN, M. L. & STEVENSON, P. R. (2012). Twins and infanticide in red howler monkeys
38 36 inhabiting a fragment in western Orinoquia. *Neotropical Primates* **19**, 41–42.
39 37
40 38 BERGER, L. R., HAWKS, J., DIRKS, P. H., ELLIOTT, M. & ROBERTS, E. M. (2017). *Homo naledi*
41 39 and Pleistocene hominin evolution in subequatorial Africa. *Elife* **6**, e24234.
42 40
43 41 BERING, J. M. (2001). Theistic percepts in other species: can chimpanzees represent the minds of
44 42 non-natural agents?. *Journal of Cognition and Culture* **1**, 107–137.
45 43
46 44 BERING, J. M., MCLEOD, K. & SHACKELFORD, T. K. (2005). Reasoning about dead agents
47 45 reveals possible adaptive trends. *Human Nature* **16**, 360–381.
48 46
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 1 BERNA, F., GOLDBERG, P., HORWITZ, L. K., BRINK, J., HOLT, S., BAMFORD, M. & CHAZAN, M.
4 2 (2012). Microstratigraphic evidence of in situ fire in the Acheulean strata of Wonderwerk Cave,
5 3 Northern Cape province, South Africa. *Proceedings of the National Academy of Sciences*,
6 4 201117620.
7
8 5
9 6 BERNSTEIN, I. S. (1968). The lutong of Kuala Selangor. *Behaviour* **32**, 1–16.
10 7
11 8 BERNSTEIN, I. S. (1975). Activity patterns in a gelada monkey group. *Folia Primatologica* **23**,
12 9 50–71.
13
14 10
15 11 BERNSTEIN, I. S. & SHARPE, L. G. (1966). Social roles in a rhesus monkey group. *Behaviour* **26**,
16 12 91–104.
17 13
18 14 BERTRAND, M. (1969). *The behavioral repertoire of the stumptail macaque: a descriptive and*
19 15 *comparative study*. Bibliotheca Primatologica, Vol 11, Karger, Basel.
20 16
21 17 BEZERRA, B. M., KEASEY, M. P., SCHIEL, N. & DA SILVA SOUTO, A. (2014). Responses towards
22 18 a dying group member in a wild New World Monkey. *Primates* **55**, 185–188.
23 19
24 20 BIRO, D. (2011). Chimpanzee mothers carry the mummified remains of their dead infants: three
25 21 case reports from Bossou. In *The chimpanzees of Bossou and Nimba*. (eds T. MATSUZAWA, T.
26 22 HUMLE and Y. SUGIYAMA), pp. 241–250. Springer, Tokyo.
27 23
28 24 BIRO, D., HUMLE, T., KOOPS, K., SOUSA, C., HAYASHI, M. & MATSUZAWA, T. (2010).
29 25 Chimpanzee mothers at Bossou Guinea carry the mummified remains of their dead infants.
30 26 *Current Biology* **20**, 351–352.
31 27
32 28 BLACKFORD, J. U., BUCKHOLTZ, J. W., AVERY, S. N. & Zald, D. H. (2010). A unique role for the
33 29 human amygdala in novelty detection. *Neuroimage* **50**, 1188–1193.
34 30
35 31 BLAIR, R. (1920). Notes on the birth of a chimpanzee. *Zoological Society Bulletin* **1**, 106–112.
36 32
37 33 BÖER, M., & SOMMER, V. (1992). Evidence for sexually selected infanticide in captive
38 34 *Cercopithecus mitis*, *Cercocebus torquatus*, and *Mandrillus leucophaeus*. *Primates* **33**, 557–563.
39 35
40 36 BOESCH, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees.
41 37 *Behaviour* **117**, 220–241.
42 38
43 39 BOESCH, C. (2012). *Wild cultures: a comparison between chimpanzee and human cultures*.
44 40 Cambridge University Press, Cambridge UK.
45 41
46 42 BOESCH, C. & BOESCH, H. (1989). Hunting behavior of wild chimpanzees in the Tai National
47 43 Park. *American journal of physical anthropology* **78**, 547–573.
48 44
49 45 BOESCH, C. & BOESCH-ACHERMANN, H. (2000). *The chimpanzees of the Tai Forest: behavioural*
50 46 *ecology and evolution*. Oxford University Press, Oxford.
51
52
53
54
55
56
57
58
59
60

- 1
2
3
4 1
5 2 BOESCH, C., BOLE, C., ECKHARDT, N. & BOESCH, H. (2010). Altruism in forest chimpanzees: the
6 3 case of adoption. *PLoS One* **5**, e8901.
7 4
8 5 BONOTI, F., LEONDARI, A. & MASTORA, A. (2013). Exploring children's understanding of death:
9 6 Through drawings and the death concept questionnaire. *Death Studies* **37**, 47–60.
10 7
11 8 BOOTH, C. (1962). Some observations on behavior of cercopithecus monkeys. *Annals of the New*
12 9 *York Academy of Sciences* **102**, 477–487.
13 10
14 11 Box, H. O. (1978). Social behaviour in the common marmoset monkey. *Biology and Human*
15 12 *Affairs* **43**, 51–64.
16 13
17 14 BOX, H. (1984). *Primate behavior and social ecology*. Chapman and Hall Ltd, London.
18 15
19 16 BOWDICH, T. E. (1819). *Mission from cape coast castle to Ashantee: with a statistical account of*
20 17 *that kingdom and geographical notices of other parts of the interior of Africa*. John Murray,
21 18 Albemarle-Street, London.
22 19
23 20 BOYER, P. (2001). *Religion explained: The human instincts that fashion gods, spirits and*
24 21 *ancestors*. William Heinemann, New York.
25 22
26 23 BOYER, T. W., PAN, J. S. & BERTENTHAL, B. I. (2011). Infants' understanding of actions
27 24 performed by mechanical devices. *Cognition* **121**, 1–11.
28 25
29 26 BRAZELTON, T. B., KOSLOWSKI, B. & MAIN, M. (1974). The origins of reciprocity: The early
30 27 mother–infant interaction. In *The Effect of the Infant on its Caregiver* (eds M. LEWIS and L.A.
31 28 ROSENBLUM), pp. 49–76. Wiley, New York.
32 29
33 30 BRONIKOWSKI, A. M., ALTMANN, J., BROCKMAN, D. K., CORDS, M., FEDIGAN, L. M., PUSEY, A.,
34 31 STOINSKI, T., MORRIS, W. F., STRIER, K. B. & ALBERTS, S. C. (2011). Aging in the natural
35 32 world: comparative data reveal similar mortality patterns across primates. *Science* **331**, 1325–
36 33 1328.
37 34
38 35 BROWN, A. E. (1879). Grief in the chimpanzee. *The American Naturalist* **13**, 173–175.
39 36
40 37 BUHL, J. S., AURE, B., RUIZ-LAMBIDES, A., GONZALEZ-MARTINEZ, J., PLATT, M. L. & BRENT, L.
41 38 J. (2012). Response of rhesus macaques (*Macaca mulatta*) to the body of a group member that
42 39 died from a fatal attack. *International Journal of Primatology* **33**, 860–871.
43 40
44 41 BURBRIDGE, B. (1928). *Gorilla, tracking and capturing the ape-man of Africa*. Century
45 42 Company, New York.
46 43
47 44 BURKART, J. M. & HESCHL, A. (2007). Understanding visual access in common marmosets,
48 45 *Callithrix jacchus*: perspective taking or behaviour reading?. *Animal Behaviour* **73**, 457–469.
49 46
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 1 BURKART, J., KUPFERBERG, A., GLASAUER, S. & VAN SCHAİK, C. (2012). Even simple forms of
4 2 social learning rely on intention attribution in marmoset monkeys (*Callithrix jacchus*). *Journal of*
5 3 *Comparative Psychology* **126**, 129–138.
6 4
7 5 BURKHARDT, R. W. (1999). Ethology, natural history, the life sciences, and the problem of place.
8 6 *Journal of the History of Biology* **32**, 489–508.
9 7
10 8 BUTTELMANN, D., BUTTELMANN, F., CARPENTER, M., CALL, J. & TOMASELLO, M. (2017). Great
11 9 apes distinguish true from false beliefs in an interactive helping task. *PLoS One* **12**, e0173793.
12 10
13 11 BUTLER, R. (1964). The reactions of rhesus monkeys to fear-provoking stimuli. *Journal of*
14 12 *Genetic Psychology* **104**, 321–330.
15 13
16 14 BYGOTT, J. D. (1972). Cannibalism among wild chimpanzees. *Nature* **238**, 410–411.
17 15
18 16 BYRNE, R. W. (2016). *Evolving insight*. Oxford University Press, Oxford.
19 17
20 18 CACCIATORE, J., RÅDESTAD, I. & FREDERIK FRØEN, J. (2008). Effects of contact with stillborn
21 19 babies on maternal anxiety and depression. *Birth* **35**, 313–320.
22 20
23 21 CALL, J., HARE, B., CARPENTER, M. & TOMASELLO, M. (2004). ‘Unwilling’ versus ‘unable’:
24 22 Chimpanzees’ understanding of human intentional action. *Developmental Science* **7**, 488–498.
25 23
26 24 CALL, J. & TOMASELLO, M. (2008). Does the chimpanzee have a theory of mind? 30 years later.
27 25 *Trends in Cognitive Sciences* **12**, 187–192.
28 26
29 27 CAMPBELL, L. A. D., TKACZYNSKI, P. J., MOUNA, M., QARRO, M., WATERMAN, J. & MAJOLO,
30 28 B. (2016). Behavioral responses to injury and death in wild barbary macaques (*Macaca*
31 29 *sylvanus*). *Primates* **57**, 309–315.
32 30
33 31 CANTELOUP, C. & MEUNIER, H. (2017). ‘Unwilling’ versus ‘unable’: Tonkean macaques’
34 32 understanding of human goal-directed actions. *PeerJ* **5**, e3227.
35 33
36 34 CARAMAZZA, A. & SHELTON, J. R. (1998). Domain-specific knowledge systems in the brain: The
37 35 animate-inanimate distinction. *Journal of Cognitive Neuroscience* **10**, 1–34.
38 36
39 37 CARBONELL, E. & MOSQUERA, M. (2006). The emergence of a symbolic behaviour: the
40 38 sepulchral pit of Sima de los Huesos, Sierra de Atapuerca, Burgos, Spain. *Comptes Rendus*
41 39 *Palevol* **5**, 155–160.
42 40
43 41 CAREY, S. (1985). *Conceptual change in childhood*. MIT Press, Cambridge, MA.
44 42
45 43 CAREY, S. (2009). *The origin of concepts*. Oxford University Press, New York.
46 44
47 45 CARPENTER, C. R. (1959). History of the monkey colony of Cayo Santiago. Transcript of lecture
48 46 given at the University of Puerto Rico Medical School, San Juan, Puerto Rico, August, 1959.
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3
4 1
5 2 CHAI, W., LU, J., WANG, Z., GUO, W. & KUANG, S. (2013). Observation on Dead-Infant-
6 3 Carrying Behavior of Rhesus Macaques in Mt. Taihangshan Area, Jiyuan, China. *Sichuan*
7 4 *Journal of Zoology* **32**, 250–252. (Chinese with English Summary).
8 5
9 6 CHEN, R. & LI, K. (2011). A case study on prolonged caring of dead infant in tibetan macaque in
10 7 Huangshan, China. *Chinese Journal of Wildlife* **32**, 11–13.
11 8
12 9 CHENEY, D. L. & SEYFARTH, R. M. (1990). How monkeys see the world: Inside the mind of
13 10 another species. University of Chicago Press, Chicago.
14 11
15 12 CHENEY, D. L. & SEYFARTH, R. M. (2007). *Baboon metaphysics: The evolution of a social mind*.
16 13 University of Chicago Press, Chicago.
17 14
18 15 CIANI, A. C. (1984). A case of infanticide in a free-ranging group of rhesus monkeys (*Macaca*
19 16 *mulatta*) in the Jackoo Forest, Simla, India. *Primates* **25**, 372–377.
20 17
21 18 CIBOT, M., SABIITI T. & MCLENNAN, M.R. (2017) Two cases of chimpanzees interacting with
22 19 dead animals without food consumption at Bulindi, Hoima District, Uganda. *Pan Africa News*
23 20 **24**, 6–8.
24 21
25 22 CLARKE, M. R. (1983). Brief report: infant - killing and infant disappearance following male
26 23 takeovers in a group of free - ranging howling monkeys (*Alouatta palliata*) in Costa Rica.
27 24 *American Journal of Primatology* **5**, 241–247.
28 25
29 26 COOLIDGE, H. J. (1933). Notes on a family of breeding gibbons. *Human Biology* **5**, 288–294.
30 27
31 28 CORDS, M. & FULLER, J. L. (2010). Infanticide in *Cercopithecus mitis stuhlmanni* in the
32 29 Kakamega Forest, Kenya: variation in the occurrence of an adaptive behavior. *International*
33 30 *Journal of Primatology* **31**, 409–431.
34 31
35 32 COWGILL, U. M. (1972). Death in *Perodicticus*. *Primates* **13**, 251–256.
36 33
37 34 CROFOOT M. C. (2012). Why mob? Reassessing the costs and benefits of primate predator
38 35 harassment. *Folia Primatologica* **83**, 252–273.
39 36
40 37 CRONIN, K. A., VAN LEEUWEN, E. J. C., MULENGA, I. C. & BODAMER, M. D. (2011). Behavioral
41 38 response of a chimpanzee mother toward her dead infant. *American Journal of Primatology* **73**,
42 39 415–421.
43 40
44 41 CROSS, D. J., MARZLUFF, J. M., PALMQUIST, I., MINOSHIMA, S., SHIMIZU, T. & MIYAOKA, R.
45 42 (2013). Distinct neural circuits underlie assessment of a diversity of natural dangers by American
46 43 crows. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20131046.
47 44
48 45 CULOT, L., LLEDO-FERRER, Y., HOELSCHER, O., LAZO, F. J. M., HUYNEN, M. C. & HEYMANN,
49 46 E. W. (2011). Reproductive failure, possible maternal infanticide, and cannibalism in wild
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 1 moustached tamarins, *Saguinus mystax*. *Primates* **52**, 179–186.
4 2
5 3 CURIO, E. (1978). The adaptive significance of avian mobbing. I. Teleonomic hypotheses and
6 4 predictions. *Zeitschrift für Tierpsychologie* **48**, 175–183.
7 5
8 6 DARWIN, C. (1871). *The descent of man*. John Murray, London.
9 7
10 8 DARWIN, C. (1872). *The expression of emotions in man and animals*. John Murray, London
11 9
12 10 DAS, S., ERINJERY, J.J. DESAI, N., MOHAN, K., KUMARA, H. N. & SINGH, M. (2018). Deceased-
13 11 infant carrying in nonhuman anthropoids: insights from systematic analysis and case studies of
14 12 Bonnet macaques (*Macaca radiata*) and Lion-tailed macaques (*Macaca silenus*). *Journal of*
15 13 *Comparative Psychology*. Advance online publication: <http://dx.doi.org/10.1037/com0000140>.
16 14
17 15 DAUM, M. M. & GREDEBÄCK, G. (2011). Spatial cueing by referential human gestures, arrows
18 16 and mechanical devices. *International Journal of Mind, Brain and Cognition* **2**, 113–126.
19 17
20 18 DEVORE, I. (1963). Mother-infant relations in free-ranging baboons. In *Maternal Behavior in*
21 19 *Mammals* (ed H.L. Rheingold), pp. 305–335. John Wiley & Sons, New York.
22 20
23 21 DE MARCO, A., COZZOLINO, R. & THIERRY, B. (2018). Prolonged transport and cannibalism of
24 22 mummified infant remains by a Tonkean macaque mother. *Primates* **59**, 55–59.
25 23
26 24 DE WAAL, F. B. M. (1986). The brutal elimination of a rival among captive male chimpanzees.
27 25 *Ethology and Sociobiology* **7**, 237–251.
28 26
29 27 DE WAAL, F. B. M. (1996). *Good natured: the origins of right and wrong in humans and other*
30 28 *animals*. Harvard University Press, Cambridge MA.
31 29
32 30 DE WAAL, F. B. M. (2001). *The ape and the sushi master: Cultural reflections of a primatologist*.
33 31 Basic Books, New York.
34 32
35 33 DE WAAL, F. B. M. (2008). Putting the altruism back into altruism: the evolution of empathy.
36 34 *Annual Review of Psychology* **59**, 279–300.
37 35
38 36 DE WAAL, F. B. M. (2013). *The bonobo and the atheist: in search of humanism among the*
39 37 *primates*. WW Norton & Company, New York
40 38
41 39 DELLATORE, D. F., WAITT, C. D. & FOITOVA, I. (2009). Two cases of mother–infant cannibalism
42 40 in orangutans. *Primates* **50**, 277–281.
43 41
44 42 DIGBY, L. (1995). Infant care, infanticide, and female reproductive strategies in polygynous
45 43 groups of common marmosets (*Callithrix jacchus*). *Behavioral Ecology and Sociobiology* **37**,
46 44 51–61.
47 45
48 46 DIRKS, P. H., BERGER, L. R., ROBERTS, E. M., KRAMERS, J. D., HAWKS, J., RANDOLPH-QUINNEY,
49 50
50 51
51 52
52 53
53 54
54 55
55 56
56 57
57 58
58 59
59 60
60

- 1
2
3 1 P. S, ELLIOT, M., MUSIBA, C. M., CHURCHILL, E. S., DE RUITER, D. J., SCHMID, P., BACKWELL, L.
4 2 R., BELYANIN, G. A., BOSHOF, P., HUNTER, K. L., *et al.* (2015). Geological and taphonomic
5 3 context for the new hominin species *Homo naledi* from the Dinaledi Chamber, South Africa.
6 4 *Elife* **4**, e09561.
7 5
8 6 DUKAS, R. & CLARK, C. W. (1995). Sustained vigilance and animal performance. *Animal*
9 7 *Behaviour* **49**, 1259–1267.
10 8
11 9 EMERY, N. J. (2000). The eyes have it: the neuroethology, function and evolution of social gaze.
12 10 *Neuroscience & Biobehavioral Reviews* **24**, 581–604.
13 11
14 12 ENGH, A. L., BEEHNER, J. C., BERGMAN, T. J., WHITTEN, P. L., HOFFMEIER, R. R., SEYFARTH, R.
15 13 M. & CHENEY, D. L. (2006). Behavioural and hormonal responses to predation in female chacma
16 14 baboons (*Papio hamadryas ursinus*). *Proceedings of the Royal Society of London B: Biological*
17 15 *Sciences* **273**, 707–712.
18 16
19 17 FAIRGRIEVE, C. (1995). Infanticide and infant eating in the blue monkey (*Cercopithecus mitis*
20 18 *stuhlmanni*) in the Budongo Forest Reserve, Uganda. *Folia Primatologica* **64**, 69–72.
21 19
22 20 FARRONI, T., JOHNSON, M. H. & CSIBRA, G. (2004). Mechanisms of eye gaze perception during
23 21 infancy. *Journal of Cognitive Neuroscience* **16**, 1320–1326.
24 22
25 23 FASHING, P. J., NGUYEN, N., BARRY, T. S., GOODALLE, C. B., BURKE, R. J., JONES, S. C. Z.,
26 24 KERBY, J. T., LEE, L. M., NURMI, N. O. & VENKATA, V. V. (2011). Death among Geladas
27 25 (*Theropithecus gelada*): a broader perspective on mummified infants and primate thanatology.
28 26 *American Journal of Primatology* **73**, 405–409.
29 27
30 28 FAWCETT, K. & MUHUMUZA, G. (2000). Death of a wild chimpanzee community member:
31 29 possible outcome of intense sexual competition. *American Journal of Primatology* **51**, 243–247.
32 30
33 31 FERNANDEZ-DUQUE, E., DI FIORE, A. & HUCK, M. (2012). The behavior, ecology, and social
34 32 evolution of New World monkey. In *The evolution of primate societies*. (eds J. Mitani, J. Call, P.
35 33 M. KAPPERLER, R. A. PALOMBIT and J. B. SILK), pp. 43-64. University of Chicago Press,
36 34 Chicago.
37 35
38 36 FLOMBAUM, J. I. & SANTOS, L. R. (2005). Rhesus monkeys attribute perceptions to others.
39 37 *Current Biology* **15**, 447–452.
40 38
41 39 FOUTS, R. S. & MILLS, S. T. (1997). *Next of kin: what chimpanzees have taught me about who*
42 40 *we are*. William Morrow & Co, New York.
43 41
44 42 FORBES, J. (1813). *Oriental Memoirs*. White Cochrane, London.
45 43
46 44 FOSSEY, D. (1983). *Gorillas in the mist*. Houghton Mifflin Harcourt, New York.
47 45
48 46 FOSSEY, D. (1984). Infanticide in mountain gorillas (*Gorilla gorilla berengei*) with comparative
49 50
50 51
51 52
52 53
53 54
54 55
55 56
56 57
57 58
58 59
59 60
60

- 1
2
3 1 notes on chimpanzees. In *Infanticide: Comparative and evolutionary perspectives* (eds G.
4 2 HAUSFATER and S.B. HRDY), pp. 217–235. Aldine Hawthorne, New York.
5 3
6 4 FOWLER, A. & HOHMANN, G. (2010). Cannibalism in wild bonobos (*Pan paniscus*) at Lui
7 5 Kotale. *American Journal of Primatology* **72**, 509–514.
8 6
9 7 GALLUP, G. G. (1979). Self-awareness in primates. *American Scientist* **67**, 417–421.
10 8
11 9 GALLUP, G. G. (1998). Self-awareness and the evolution of social intelligence. *Behavioural*
12 10 *Processes* **42**, 239–247.
13 11
14 12 GARCÍA-FERIA, L. M., PÉREZ, B. A. C. & SÁNCHEZ-GIRÓN, X. (2015). New record of infanticide
15 13 in *Alouatta pigra*: chance of betrayal of altruism. *THERYA* **7**, 193–196.
16 14
17 15 GARNER, R. L. (1900). *Apes and monkeys: their life and language*. Ginn & Company, Boston.
18 16
19 17 GHAZANFAR, A. A. & SANTOS, L. R. (2004). Primate brains in the wild: the sensory bases for
20 18 social interactions. *Nature Reviews Neuroscience* **5**, 603–616.
21 19
22 20 GIBSON, K. N., VICK, L. G., PALMA, A. C., CARRASCO, F. M., TAUB, D. & RAMOS-FERNÁNDEZ,
23 21 G. (2008). Intra-community infanticide and forced copulation in spider monkeys: a multi-site
24 22 comparison between Cocha Cashu, Peru and Punta Laguna, Mexico. *American Journal of*
25 23 *Primatology* **70**, 485–489.
26 24
27 25 GILBERT, P. (2015). The evolution and social dynamics of compassion. *Social and Personality*
28 26 *Psychology Compass* **9**, 239–254.
29 27
30 28 GILMER, W. S. & MCKINNEY, W. T. (2003). Early experience and depressive disorders: human
31 29 and non-human primate studies. *Journal of Affective Disorders* **75**, 97–113.
32 30
33 31 GONÇALVES, A. & BIRO, D. (2018). Comparative thanatology, an integrative approach: exploring
34 32 sensory/cognitive aspects of death recognition in vertebrates and invertebrates. *Philosophical*
35 33 *Transactions of the Royal Society B: Biological Sciences* **373**, 20170263.
36 34
37 35 GOODALL, J. (1977). Infant killing and cannibalism in free-living chimpanzees. *Folia*
38 36 *Primatologica* **28**, 259–282.
39 37
40 38 GOODALL, J. (1986). *Chimpanzees of Gombe: patterns of behaviour*. Harvard University Press,
41 39 Cambridge M.A.
42 40
43 41 GREEN, S. (1975). Variation of vocal pattern with social situation in the Japanese monkey
44 42 (*Macaca fuscata*): a field study. In *Primate behavior* Vol 4 (ed L.A. ROSENBLUM.), pp. 1–102.
45 43 Academic Press, New York.
46 44
47 45 GOODALL, J. (1990). *Through a window: my thirty years with the chimpanzees of Gombe*.
48 46 Houghton Mifflin Harcourt, New York.
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3
4 1
5 2 GUO, D., QI, X., TIAN, J., HU, Y., SI, K., GAO, C. & LI, B. (2016). Carrying of dead infants by
6 3 Golden Snub-nosed Monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains. *Acta*
7 4 *Theriologica Sinica* **36**, 177–183.
- 8 5
9 6 GUPTA, A. K. (2000). Behaviour of Phayre's langur (*Trachypithecus phayrei*) on the death of
10 7 one adult female. *Mammalia* **64**, 477–480.
- 11 8
12 9 HAGENAARS, M. A., OITZL, M. & ROELOFS, K. (2014). Updating freeze: aligning animal and
13 10 human research. *Neuroscience and Biobehavioral Reviews* **47**, 165–176.
- 14 11
15 12 HAMBURG, D. A. (1972). Aggressive behavior of chimpanzees and baboons in natural habitats.
16 13 In *Principles, Practices, and Positions in Neuropsychiatric Research* (eds J. V. Brady and W. J.
17 14 H. Nauta), pp. 385–398. Pergamon Press Ltd, Oxford.
- 18 15
19 16 HANAMURA, S., KIYONO, M., LUKASIK-BRAUM, M., MLENGEYA, T., FUJIMOTO, M., NAKAMURA,
20 17 M. & NISHIDA, T. (2008). Chimpanzee deaths at Mahale caused by a flu-like disease. *Primates*
21 18 **49**, 77–80.
- 22 19
23 20 HANAMURA, S., KOORIYAMA, T. & HOSAKA, K. (2015). Diseases and deaths: variety and impact
24 21 on social life. In *Mahale chimpanzees 50 years of research* (eds M. NAKAMURA, K. HOSAKA and
25 22 K. ZAMMA), pp. 354–371. Cambridge University Press, Cambridge.
- 26 23
27 24 HARE, B., ADDESSI, E., CALL, J., TOMASELLO, M. & VISALBERGHI, E. (2003). Do capuchin
28 25 monkeys, *Cebus apella*, know what conspecifics do and do not see?. *Animal Behaviour* **65**, 131–
29 26 142.
- 30 27
31 28 HARE, B., CALL, J., AGNETTA, B. & TOMASELLO, M. (2000). Chimpanzees know what
32 29 conspecifics do and do not see. *Animal Behaviour* **59**, 771–785.
- 33 30
34 31 HARE, B., CALL, J. & TOMASELLO, M. (2001). Do chimpanzees know what conspecifics know?.
35 32 *Animal Behaviour* **61**, 139–151.
- 36 33
37 34 HASEGAWA, T., HIRAIWA, M., NISHIDA, T. & TAKASAKI, H. (1983). New evidence on
38 35 scavenging behavior in wild chimpanzees. *Current Anthropology* **24**, 231–232.
- 39 36
40 37 HAUSER, M. D. (1998). A nonhuman primate's expectations about object motion and destination:
41 38 The importance of self-propelled movement and animacy. *Developmental Science* **1**, 31–37.
- 42 39
43 40 HAUSFATER, G. (1976). Predatory behavior of yellow baboons. *Behaviour* **56**, 44–67.
- 44 41
45 42 HEBB, D. O. (1946). On the nature of fear. *Psychological Review* **53**, 259–276.
- 46 43
47 44 HILÁRIO, R. R. & FERRARI, S. F. (2010). Double infanticide in a free-ranging group of buffy-
48 45 headed marmosets, *Callithrix flaviceps*. *Journal of Ethology* **28**, 195–199.
- 49 46
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 1 HINDE, R. A., SPENCER-BOOTH, Y., & BRUCE, M. (1966). Effects of 6-day maternal deprivation
4 2 on rhesus monkey infants. *Nature* **210**, 1021–1023.
5 3
6 4 HIRAIWA-HASEGAWA, M., BYRNE, R. W., TAKASAKI, H. & BYRNE, J. M. (1986). Aggression
7 5 toward large carnivores by wild chimpanzees of Mahale Mountains National Park, Tanzania.
8 6 *Folia Primatologica* **47**, 8–13.
9 7
10 8 HIRATA, S. & MIZUNO, Y. (2011). Animal toying. In *The Chimpanzees of Bossou and Nimba*
11 9 (eds T. MATSUZAWA, T. HUMLE and Y. SUGIYAMA), pp. 137–141. Springer, Tokyo.
12 10
13 11 HIRATA, S., YAMAKOSHI, G., FUJITA, S., OHASHI, G. & MATSUZAWA, T. (2001). Capturing and
14 12 toying with hyraxes (*Dendrohyrax dorsalis*) by wild chimpanzees (*Pan troglodytes*) at Bossou,
15 13 Guinea. *American Journal of Primatology* **53**, 93–97.
16 14
17 15 HOAGE, R. F. & DEISS, W. A. (1996). *New worlds, new animals. From menagerie to zoological*
18 16 *parks in the Nineteenth century*. John Hopkins University Press, London.
19 17
20 18 HOFER, A., HUFFMAN, M. A. & ZIESLER, G. (2000). *Mahale: A Photographic Encounter with*
21 19 *Chimpanzees*. Sterling Publishing Co., New York.
22 20
23 21 HOFER, T., HAUF, P. & ASCHERSLEBEN, G. (2005). Infant's perception of goal-directed actions
24 22 performed by a mechanical device. *Infant Behavior and Development* **28**, 466–480.
25 23
26 24 HOFF, M. P., HOFF, K. T. & MAPLE, T. L. (1998). Behavioural response of a Western lowland
27 25 gorilla *Gorilla gorilla gorilla* group to the loss of the silverback male at Zoo Atlanta.
28 26 *International Zoo Yearbook* **36**, 90–96.
29 27
30 28 HOLLOWAY, R. L. (2015). Brain Evolution. In *Basics in Human Evolution* (ed. Muehlenbein, M.
31 29 P.), pp. 235–250. Elsevier, London.
32 30
33 31 HOSAKA, K., MATSUMOTO-ODA, A., HUFFMAN, M. A. & KAWANAKA, K. (2000). Reactions to
34 32 dead bodies of conspecifics by wild chimpanzees in the Mahale Mountains, Tanzania. *Primate*
35 33 *Research* **16**, 1–15. (Japanese with English Summary).
36 34
37 35 HOSAKA, K., INOUE, E. & FUJIMOTO, M. (2014). Responses of wild chimpanzees to fresh
38 36 carcasses of armadillo (*Oryzomys azer*) in Mahale. *Pan Africa News* **21**, 19–22.
39 37
40 38 HOUZEAU, J. C. (1872). *Études sur les facultés mentales des animaux comparées à celles de*
41 39 *L'homme*. Tome II. Hector Manceaux, Paris. (in French).
42 40
43 41 HRDY, S. B. (1974). Male-male competition and infanticide among the langurs (*Presbytis*
44 42 *entellus*) of Abu, Rajasthan. *Folia Primatologica* **22**, 19–58.
45 43
46 44 HRDY, S. B. (2000). *Mother nature: maternal instincts and how they shape the human species*.
47 45 Ballantine Books, New York.
48 46
49 47
50 48
51 49
52 50
53 51
54 52
55 53
56 54
57 55
58 56
59 57
60 58

- 1
2
3 1 HSIANG–JEN, S. & HSIU–HUI, S. (2008). Cannibalism of mother Taiwanese macaque (*Macaca*
4 2 *cyclopis*) on infant corpse at Mt. Chai. *Endemic Biological Research* **10**, 35–40. (Chinese with
5 3 English Summary).
6 4
7 4
8 5 HUBLIN, J. J. (2009). The prehistory of compassion. *Proceedings of the National Academy of*
9 6 *Sciences* **106**, 6429–6430.
10 7
11 8 HUMPHREYS, R. K. & RUXTON, G. D. (2018). A review of thanatosis (death feigning) as an anti-
12 9 predator behaviour. *Behavioral Ecology and Sociobiology* **72**, 22.
13
14 10
15 11 HUNTER, S. B. & SMITH, D. E. (2008). Predictors of children’s understandings of death: Age,
16 12 cognitive ability, death experience and maternal communicative competence. *OMEGA–Journal*
17 13 *of Death and Dying* **57**, 143–162.
18 14
19 15 IIDA, T. (1999). Predation of Japanese macaque *Macaca fuscata* by mountain hawk eagle
20 16 *Spizaetus nipalensis*. *Japanese Journal of Ornithology* **47**, 125–127.
21 17
22 18
23 18 IURCK, M. F., COSTA, L. C. M., STRIER, K. B. & GOMES, M. L. F. (2005). Relato do
24 19 comportamento materno de uma fêmea muriqui primípara (*Brachyteles arachnoides*, E.
25 20 Geoffroy, 1806) (Primates, Atelidae) com um filhote morto de quatro dias no semi-cativeiro do
26 21 Passeio Público, Curitiba, Paraná. *Congresso Brasileiro de Primatologia, 2005, Porto Alegre.*
27 22 *Anais do Congresso Brasileiro de Primatologia*, p. 112. (in Portuguese).
28 23
29 24
30 24 IZAR, P., RAMOS-DA-SILVA, E. D., DE-RESENDE, B. D. & OTTONI, E. B. (2007). A case of
31 25 infanticide in tufted capuchin monkeys (*Cebus nigritus*). *Mastozoologia Neotropical* **14**, 73–76.
32 26
33 27
34 27 IZAWA, K. (1992). Social changes within a group of wild black-capped capuchins (*Cebus apella*)
35 28 (III). *Field Studies of New World Monkeys, La Macarena, Colombia* **7**, 9–14.
36 29
37 30
38 30 JASTORFF, J., POPIVANOV, I. D., VOGELS, R., VANDUFFEL, W. & ORBAN, G. A. (2012).
39 31 Integration of shape and motion cues in biological motion processing in the monkey STS.
40 32 *Neuroimage* **60**, 911–921.
41 33
42 34
43 34 JAY, P. C. (1962). Aspects of maternal behavior among langurs. *Annals of the New York*
44 35 *Academy of Sciences* **102**, 468–476.
45 36
46 37
47 37 JENKS, A. E. (1911). The Bulu Knowledge of the Chimpanzee and Gorilla. *American*
48 38 *Anthropologist* **13**, 56–64.
49 39
50 40
51 40 JENSEN, G.D. & TOLMAN, C.W. (1962). Mother-infant relationship in the monkey, *Macaca*
52 41 *nemestrina*: The effect of brief separation and mother-infant specificity. *Journal of Comparative*
53 42 *and Physiological Psychology* **55**, 131–136.
54 43
55 44
56 44 JOHNSON, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience* **6**, 766.
57 45
58 46
59 46 JOHNSON, M. H. (2006). Biological motion: a perceptual life detector?. *Current Biology* **16**,
60

- 1 R376–R377.
- 2
- 3
- 4
- 5
- 6 JOHNSTON, H. (1885). The Kilimanjaro expedition. *Science* **5**, 152–154.
- 7
- 8
- 9 KAMEWARI, K., KATO, M., KANDA, T., ISHIGURO, H. & HIRAKI, K. (2005). Six-and-a-half-
- 10 month-old children positively attribute goals to human action and to humanoid-robot motion.
- 11 *Cognitive Development* **20**, 303–320.
- 12
- 13
- 14 KANNGIESSER, P., SUEUR, C., RIEDL, K., GROSSMANN, J. & CALL, J. (2011). Grooming network
- 15 cohesion and the role of individuals in a captive chimpanzee group. *American journal of*
- 16 *primatology* **73**, 758–767.
- 17
- 18
- 19 KANO, T. (1992). *The last ape: pygmy chimpanzee behavior and ecology*. Stanford University
- 20 Press, Standford.
- 21
- 22
- 23 KAPLAN, J. (1973). Responses of mother squirrel monkeys to dead infants. *Primates* **14**, 89–91.
- 24
- 25
- 26 KAPLAN, G., PINES, M. K. & ROGERS, L. J. (2012). Stress and stress reduction in common
- 27 marmosets. *Applied Animal Behaviour Science* **137**, 175–182.
- 28
- 29
- 30
- 31 KARG, K., SCHMELZ, M., CALL, J. & TOMASELLO, M. (2015). The goggles experiment: can
- 32 chimpanzees use self-experience to infer what a competitor can see?. *Animal Behaviour* **105**,
- 33 211–221.
- 34
- 35
- 36 KASTENBAUM, R. (2000). *The psychology of death*. Springer Publishing Company, New York.
- 37
- 38
- 39
- 40 KAUFMAN, C. I. & ROSENBLUM, L. A. (1967). The reaction to separation in infant monkeys:
- 41 anaclitic depression and conservation-withdrawal. *Psychosomatic Medicine* **29**, 648–675.
- 42
- 43
- 44
- 45 KAWAI, M. (1960). A field experiment on the process of group formation in the Japanese
- 46 monkey (*Macaca fuscata*), and the releasing of the group at Ohirayama. *Primates* **2**, 181–255.
- 47
- 48
- 49
- 50 KEENAN, S., MATHEVON, N., STEVENS, J. M., GUÉRY, J. P., ZUBERBÜHLER, K. & LEVRÉRO, F.
- 51 (2016). Enduring voice recognition in bonobos. *Scientific Reports* **6**, 22046.
- 52
- 53
- 54
- 55 KENYON, B. (2001). Current research in children's conceptions of death: a critical review.
- 56 *Omega: Journal of Death and Dying* **43**, 63–91.
- 57
- 58
- 59
- 60
- 61
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- 63
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- 67
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3
4 1
5 2 KING, G. & STEKLIS, H. (1984). New evidence for the craniocervical killing bite in primates.
6 3 *Journal of Human Evolution* **13**, 469–481.
7 4
8 5 KING, G. & STEKLIS, H. (2008). The craniocervical bite in chimpanzees and baboons. *Human*
9 6 *Evolution* **23**, 183–186.
10 7
11 8 KIPLING, J. L. (1891). *Beast and man in India: a popular sketch of Indian animals in their*
12 9 *relations with the people*. Macmillan and Company, London.
13 10
14 11 KOERTH-BAKER, M. (2013). Want to Understand Mortality? Look to the Chimps. The New York
15 12 Times. Retrieved from [https://www.nytimes.com/2013/06/30/magazine/want-to-understand-](https://www.nytimes.com/2013/06/30/magazine/want-to-understand-mortality-look-to-the-chimps.html)
16 13 [mortality-look-to-the-chimps.html](https://www.nytimes.com/2013/06/30/magazine/want-to-understand-mortality-look-to-the-chimps.html)
17 14
18 15 KOFORD, C. B. (1965). Population dynamics of rhesus monkeys on Cayo Santiago. In *Primate*
19 16 *Behavior*, (ed I. DEVORE), pp. 160–174. Holt, Rinehart, & Winston, New York.
20 17
21 18 KOORIYAMA, T. (2009). The death of a newborn chimpanzee at Mahale: reactions of its mother
22 19 and other individuals to the body. *Pan Africa News* **16**, 19–21.
23 20
24 21 KORTLANDT, A. (1967). Experimentation with Chimpanzees in the Wild. In *Neue Ergebnisse der*
25 22 *Primatologie* (eds D. STARCK, R. SCHNIDER and H.J. KUHN), pp. 208–244. Stuttgart, Fischer,
26 23
27 24 KRIEGESKORTE, N., MUR, M., RUFF, D. A., KIANI, R., BODURKA, J., ESTEKY, H. & BANDETTINI,
28 25 P. A. (2008). Matching categorical object representations in inferior temporal cortex of man and
29 26 monkey. *Neuron* **60**, 1126–1141.
30 27
31 28 KRUPENYE, C., KANO, F., HIRATA, S., CALL, J. & TOMASELLO, M. (2016). Great apes anticipate
32 29 that other individuals will act according to false beliefs. *Science* **354**, 110–114.
33 30
34 31 KUMARAN, D. & MAGUIRE, E. A. (2007). Match–mismatch processes underlie human
35 32 hippocampal responses to associative novelty. *Journal of Neuroscience* **27**, 8517–8524.
36 33
37 34 KUPFERBERG, A., GLASAUER, S. & BURKART, J. M. (2013). Do robots have goals? How agent
38 35 cues influence action understanding in non-human primates. *Behavioural Brain Research* **246**,
39 36 47–54.
40 37
41 38 LAZARO-PEREA, C., CASTRO, C. S., HARRISON, R., ARAUJO, A., ARRUDA, M. F. & SNOWDON, C.
42 39 T. (2000). Behavioral and demographic changes following the loss of the breeding female in
43 40 cooperatively breeding marmosets. *Behavioral Ecology and Sociobiology* **48**, 137–146.
44 41
45 42 LEGERSTEE, M. & MARKOVA, G. (2008). Variations in imitation: Ten-month-old infant
46 43 awareness of intentional action. *Infant Behavior and Development* **31**, 81–91.
47 44
48 45 LESLIE, A. M. (1994). ToMM, ToBy, and Agency: Core architecture and domain specificity. In
49 46 *Mapping the mind: Domain Specificity in Cognition and Culture*. (eds L. A. HIRSCHFELD and S.

- 1
2
3 1 A. GELMAN), pp. 119-148. Cambridge University Press, Cambridge.
4 2
5 3 LESS, E. H., LUKAS, K. E., KUCHAR, C. W. & STOINSKI, T. S. (2010). Behavioral response of
6 4 captive western lowland gorillas (*Gorilla gorilla gorilla*) to the death of silverbacks in multi-
7 5 male groups. *Zoo Biology* **29**, 16–29.
8 6
9 7 LI, T., REN, B., LI, D., ZHANG, Y. & LI, M. (2012). Maternal responses to dead infants in
10 8 Yunnan snub-nosed monkey (*Rhinopithecus bieti*) in the Baimaxueshan Nature Reserve,
11 9 Yunnan, China. *Primates* **53**, 127–132.
12
13 11 LITTLEFIELD, B. L. (2010). Infanticide following male takeover event in Verreaux's sifaka
14 12 (*Propithecus verreauxi verreauxi*). *Primates* **51**, 83–86.
15 13
16 14 LONG, Y. & KIRKPATRICK, C. R. (1994). Report on the distribution, population, and ecology of
17 15 the Yunnan snub-nosed monkey (*Rhinopithecus bieti*). *Primates* **35**, 241–250.
18 16
19 17 LONGBOTTOM, S. & SLAUGHTER, V. (2018). Sources of children's knowledge about death and
20 18 dying. *Philosophical Transactions of the Royal Society B: Biological Sciences* **373**, 20170267.
21 19
22 20 LOVERIDGE, A. (1921). Notes on east African mammalia (other than horned ungulates) collected
23 21 or kept in captivity 1915-1919. Part II. *The Journal of the East Africa and Uganda Natural*
24 22 *History Society* **5**, 39–69.
25 23
26 24 LOVERIDGE, A. (1923). Notes on East African mammals, collected 1920–1923. *Proceedings of*
27 25 *the Zoological Society of London* **93**, 685–739.
28 26
29 27 LU, J.Q., ZHAO, D.P. & LI, B. G. (2007). Prolonged carrying of a dead infant among the golden
30 28 monkey (*Rhinopithecus roxelanna*) in the Qinling Mountains, China. *Acta Zoologica Sinica* **53**,
31 29 175–178. (Chinese with English Summary).
32 30
33 31 MACLEAN, E. L. & HARE, B. (2012). Bonobos and chimpanzees infer the target of another's
34 32 attention. *Animal Behaviour* **83**, 345–353.
35 33
36 34 MAJOLO, B. & MCFARLAND, R. (2009). Brief communication: Self-suckling in Barbary macaque
37 35 (*Macaca sylvanus*) mothers before and after the death of their infant. *American Journal of*
38 36 *Physical Anthropology* **140**, 381–383.
39 37
40 38 MARAIS, E. (1969). *The soul of the ape*. Anthony Blond, London.
41 39
42 40 MAREN, S. (2014). Fear of the unexpected: hippocampus mediates novelty-induced return of
43 41 extinguished fear in rats. *Neurobiology of Learning and Memory* **108**, 88–95.
44 42
45 43 MARKHAM, A. C., GESQUIERE, L. R., BELLENGER, J. P., ALBERTS, S. C. & ALTMANN, J. (2011).
46 44 White monkey syndrome and presumptive copper deficiency in wild savannah baboons.
47 45 *American Journal of Primatology* **73**, 1160–1168.
48 46
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 1 MARKSON, L. & SPELKE, E. S. (2006). Infants' rapid learning about self-propelled objects.
4 2 *Infancy* **9**, 45–71.
5 3
6 4 MARTIN, A. & SANTOS, L. R. (2014). The origins of belief representation: Monkeys fail to
7 5 automatically represent others' beliefs. *Cognition* **130**, 300–308.
8 6
9 7 MATSUDA, I., TUUGA, A. & HIGASHI, S. (2008). Clouded leopard (*Neofelis diardi*) predation on
10 8 proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. *Primates* **49**, 227–231.
11 9
12 10 MATSUMOTO, T., ITOH, N., INOUE, S. & NAKAMURA, M. (2016). An observation of a severely
13 11 disabled infant chimpanzee in the wild and her interactions with her mother. *Primates* **57**, 3–7.
14 12
15 13 MATSUMOTO-ODA, A. (2015). How surviving baboons behaved after leopard predation: a case
16 14 report. *Anthropological Science* **123**, 13–17.
17 15
18 16 MATSUZAWA, T. (1997). The death of an infant chimpanzee at Bossou, Guinea. *Pan Africa News*
19 17 **4**, 4–6.
20 18
21 19 MCGREW, W. C. (2004). *The cultured chimpanzee: reflections on cultural primatology*.
22 20 Cambridge University Press, Cambridge.
23 21
24 22 MCGREW, W. C. & BAEHREN, L. (2016). “Parting is such sweet sorrow”, but only for humans?.
25 23 *Human Ethology Bulletin* **31**, 5–14.
26 24
27 25 MCKENNA, J. J. (1982). The evolution of primate societies, reproduction and parenting. In
28 26 *Primate Behaviour* (eds J. L., FOBES, & J. E. KING), pp 87–133. Academic Press, London.
29 27
30 28 MELTZOFF, A. N. (1995). Understanding the intentions of others: Re-enactment of intended acts
31 29 by 18-month-old children. *Developmental Psychology* **31**, 838–850.
32 30
33 31 MERZ, E. (1978). Male-male interactions with dead infants in *Macaca sylvanus*. *Primates* **19**,
34 32 749–754.
35 33
36 34 MITTERMEIER, R. A. (1973). Group activity and population dynamics of the howler monkey on
37 35 Barro Colorado Island. *Primates* **14**, 1–19.
38 36
39 37 MOHNOT, S. M. (1971). Some aspects of social changes and infant-killing in the Hanuman
40 38 langur, *Presbytis entellus* (Primates: Cercopithecidae), in western India. *Mammalia* **35**, 175–198.
41 39
42 40 MOHNOT, S. M. (1980). Behavioral changes in Hanuman langur infant after mothers death.
43 41 *Zoologischer Anzeiger* **205**, 67–75.
44 42
45 43 MOLLIN, G. (1820). *Travels to the interior of Africa, to the sources of Senegal and Gambia:*
46 44 *performed by command of the French government, in the Year 1818*. Henry Colburn & Co,
47 45 London.
48 46
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 1 MORGAN, T. J., UOMINI, N. T., RENDELL, L. E., CHOUINARD-THULY, L., STREET, S. E., LEWIS, H.
4 2 M., CROSS, C. P., EVANS, C., KEARNEY, R., DE LA TORRE, I., WHITEN, A., & LALAND, K. N.
5 3 (2015). Experimental evidence for the co-evolution of hominin tool-making teaching and
6 4 language. *Nature Communications* **6**, 6029.
- 7 5
8 6 MORI, A., IWAMOTO, T. & BEKELE, A. (1997). A case of infanticide in a recently found gelada
9 7 population in Arsi, Ethiopia. *Primates* **38**, 79–88.
- 10 8
11 9 MORI, A., BELAY, G. & IWAMOTO, T. (2003). Changes in unit structures and infanticide
12 10 observed in Arsi geladas. *Primates* **44**, 217–223.
- 13 11
14 12 MORTON, J. & JOHNSON, M. H. (1991). CONSPEC and CONLERN: a two-process theory of
15 13 infant face recognition. *Psychological Review* **98**, 164–181.
- 16 14
17 15 MULLER, M. N., MPONGO, E., STANFORD, C. B. & BOEHM, C. (1995). A note on scavenging by
18 16 wild chimpanzees. *Folia Primatologica* **65**, 43–47.
- 19 17
20 18 MYOWA-YAMAKOSHI, M. & TOMONAGA, M. (2001). Perceiving eye gaze in an infant gibbon
21 19 (*Hylobates agilis*). *Psychologia* **44**, 24–30.
- 22 20
23 21 MYOWA-YAMAKOSHI, M., TOMONAGA, M., TANAKA M. & MATSUZAWA T. (2003). Preference
24 22 for human direct gaze in infant chimpanzees (*Pan troglodytes*). *Cognition* **89**, B53–B64.
- 25 23
26 24 NAKAGAWA, N. (2007). *The running monkeys in the savanna: ecology and society of Patas*
27 25 *monkeys*. Kyoto University Press, Kyoto. (in Japanese).
- 28 26
29 27 NAKAMICHI, M., KOYAMA, N. & JOLLY, A. (1996). Maternal responses to dead and dying Infants
30 28 in wild troops of ring-tailed lemurs at the Berenty Reserve, Madagascar. *International Journal of*
31 29 *Primatology* **17**, 505–523.
- 32 30
33 31 NAKAMICHI M. (2016). Primate Social Behavior: Understanding the Social Relationships of
34 32 Japanese Macaques. In *Cognitive Neuroscience Robotics B* (eds M. KASAKI, H. ISHIGURO, M.
35 33 ASADA, M. OSAKA, and T. FUJIKADO T.), pp. 59–100. Springer, Tokyo.
- 36 34
37 35 NASELARIS, T., STANSBURY, D. E. & GALLANT, J. L. (2012). Cortical representation of animate
38 36 and inanimate objects in complex natural scenes. *Journal of Physiology-Paris* **106**, 239–249.
- 39 37
40 38 NASH, L. T. (1974). Parturition in a feral baboon (*Papio anubis*). *Primates* **15**, 279–285.
- 41 39
42 40 NEGAYAMA, K. (1988). Effects of infant's behavior on mothers' responsiveness towards them in
43 41 *Macaca fascicularis*: an experimental analysis by anesthesia. *Primate Research* **4**, 1–10.
44 42 (Japanese with English summary).
- 45 43
46 44 NEWTON, P. N. (1986). Infanticide in an undisturbed forest population of Hanuman langurs,
47 45 *Presbytis entellus*. *Animal Behaviour* **34**, 785–789.
- 48 46
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 1 NEWTON-FISHER, N. E. (1999). Infant killers of Budongo. *Folia Primatologica* **70**, 167–169.
4 2
5 3 NEWTON-FISHER, N. E. (2015). The hunting behavior and carnivory of wild chimpanzees. In
6 4 *Handbook of Paleoanthropology* (eds W. HENKE and I. TATTERSALL), pp. 1661–1691. Springer,
7 5 Heidelberg.
8 6
9 7 NICOLSON, N. A. (1991). Maternal behavior in human and nonhuman primates. In
10 8 *Understanding behavior: What primate studies tell us about human behavior*. (eds J. D. LOY and
11 9 C. B. PETERS), pp. 17–50. Oxford University Press, Oxford.
12
13
14 10 NISHIDA, T. (1973). *The Children of the Mountain Spirits: Search for the Social Structure of*
15 11 *Chimpanzees*. Chikuma-shobo, Tokyo. (In Japanese).
16 12
17 13 NISHIDA, T. (1981). *The World of Wild Chimpanzees*. Chuko-shinsho, Tokyo. (In Japanese).
18 14
19 15 NISHIDA, T. (1994). Review of recent findings on Mahale chimpanzees: Implications and future
20 16 research directions. In *Chimpanzee Cultures*. (eds R. W. WRANGHAM, W. C. MCGREW, F. B. M.
21 17 DE WAAL and P. G. HELTNE), pp. 373–396. Harvard University Press, Cambridge.
22 18
23 19 NISHIDA, T. (1998). Deceptive Tactic by an Adult Male Chimpanzee to Snatch a Dead Infant
24 20 from its Mother. *Pan Africa News* **5**, 13–15.
25 21
26 22 NISHIDA, T. (2012). *Chimpanzees of the lakeshore: natural history and culture at Mahale*.
27 23 Cambridge University Press, Cambridge.
28 24
29 25 NOTMAN, H. & MUNN, J. (2003). A Case of infant carrying by an adult male chimpanzee in the
30 26 Budongo Forest. *Pan Africa News* **10**, 7–9.
31 27
32 28 ONDERDONK, D. A. (2000). Infanticide of a newborn black-and-white colobus monkey (*Colobus*
33 29 *guereza*) in Kibale National Park, Uganda. *Primates* **41**, 209–212.
34 30
35 31 ORBACH, I., TALMON, O., KEDEM, P. & HAR-EVEN, D. (1987). Sequential patterns of five
36 32 subconcepts of human and animal death in children. *Journal of the American Academy of Child*
37 33 *& Adolescent Psychiatry* **26**, 578–582.
38 34
39 35 ORGELDINGER, M. (1996). Behavioural changes following the death of a siamang infant.
40 36 *International Zoo News* **43**, 426–433.
41 37
42 38 OSVATH, M. (2016). Putting flexible animal prospection into context: escaping the theoretical
43 39 box. *Wiley Interdisciplinary Reviews: Cognitive Science* **7**, 5–18.
44 40
45 41 OSVATH, M. & PERSSON, T. (2013). Great apes can defer exchange: A replication with different
46 42 results suggesting future oriented behavior. *Frontiers in Psychology* **4**, 698.
47 43
48 44 PALOMBIT, R. A. (1995). Longitudinal patterns of reproduction in wild female siamang
49 45 (Hylobates syndactylus) and white-handed gibbons (*Hylobates lar*). *International Journal of*
50 46
51
52
53
54
55
56
57
58
59
60

- 1
2
3 1 *Primates* **16**, 739–760.
4 2
5 3 PALOMBIT, R. A., SEYFARTH, R. M. & CHENEY, D. L. (1997). The adaptive value of ‘friendships’
6 4 to female baboons: experimental and observational evidence. *Animal Behaviour* **54**, 599–614.
7 5
8 6 PATTERSON, F. & GORDON, W. (1993). The case for the personhood of gorillas. In *The Great*
9 7 *Ape Project* (eds P. CAVALIERI and P. SINGER), pp. 58–79. St. Martin’s Griffin, New York.
10 8
11 9 PENN, D. (2011). How folk psychology ruined comparative psychology: and how scrub jays can
12 10 save it. In *Animal thinking: contemporary issues in comparative cognition*. (eds R. MENZEL and
13 11 J. FISCHER), pp. 253–266. MIT Press, Cambridge.
14 12
15 13 PEREIRA, M. E. (1983). Abortion following the immigration of an adult male baboon (*Papio*
16 14 *cynocephalus*). *American Journal of Primatology* **4**, 93–98.
17 15
18 16 PÉREZ-MANRIQUE, A. & GOMILA, A. (2018). The comparative study of empathy: sympathetic
19 17 concern and empathic perspective-taking in non-human animals. *Biological Reviews* **93**, 248–
20 18 269.
21 19
22 20 PERRY, S. & MANSON, J. H. (2009). *Manipulative monkeys, the capuchins of Lomas Barbudal*.
23 21 Harvard University Press, Cambridge M.A.
24 22
25 23 PETTITT, P. (2011). *The Palaeolithic Origins of Human Burial*. Routledge, Abingdon.
26 24
27 25 PETTITT, P. (2015). Landscapes of the Dead: The evolution of human mortuary activity from
28 26 body to place in Palaeolithic Europe. In *Settlement, Society and Cognition in Human Evolution:*
29 27 *Landscapes in Mind*. (eds F. COWARD, R. HOSFIELD, M. POPE and F. WENBAN-SMITH), pp. 258–
30 28 274. Cambridge University Press, Cambridge.
31 29
32 30 PHILLIPS, W., BARNES, J. L., MAHAJAN, N., YAMAGUCHI, M. & SANTOS, L. R. (2009).
33 31 ‘Unwilling versus unable’: Capuchins’ (*Cebus apella*) understanding of human intentional
34 32 action. *Developmental Science* **12**, 938–945.
35 33
36 34 PIEL A.K. & STEWART F.A. (2015). Non-Human Animal Responses towards the Dead and
37 35 Death: A Comparative Approach to Understanding the Evolution of Human Mortuary Practices.
38 36 In *Death Rituals and Social Order in the Ancient World: Death Shall Have No Dominion*. (eds
39 37 C. RENFREW, M. J. BOYD and I. MORLEY), pp. 15–26. Cambridge University Press, Cambridge.
40 38
41 39 PIEROTTI, R. & ANNETT, C. (2014). We probably thought that would be true: perceiving complex
42 40 emotional states in nonhumans. *Ethnobiology Letters* **5**, 15–21.
43 41
44 42 POLLOCK, G. H. (1961). Mourning and adaptation. *International Journal of Psycho-Analysis* **43**,
45 43 341–361.
46 44
47 45 POSSAMAI, C. B., YOUNG, R. J., MENDES, S. L. & STRIER, K. B. (2007). A primiparous northern
48 46 muriqui female (*Brachyteles hypoxanthus*) carrying a dead infant. *XII Brazilian Congress of*
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 1 *Primateology*. (in Portuguese).
4 2
5 3 POULIN-DUBOIS, D., LEPAGE, A. & FERLAND, D. (1996). Infants' concept of animacy. *Cognitive*
6 4 *Development* **11**, 19–36.
7 5
8 6 PREMACK, D. (1976). Language and intelligence in ape and man: how much is the gap between
9 7 human and animal intelligence narrowed by recent demonstrations of language in chimpanzees?.
10 8 *American Scientist* **64**, 674–683.
11 9
12 10 PRESCOTT, M. J. (2010). Ethics of primate use. *Advances in Science and Research* **5**, 11–22.
13 11
14 12 PRICE, E. C. (1990). Parturition and perinatal behaviour in captive cotton-top tamarins (*Saguinus*
15 13 *oedipus*). *Primates* **31**, 523–535.
16 14
17 15 PRINCE-HUGHES, D. (2001). *Gorillas Among Us: A Primate Ethnographer's Book of Days*.
18 16 University of Arizona Press, Tucson.
19 17
20 18 PRUETZ, J. D. (2011). Targeted helping by a wild adolescent male chimpanzee (*Pan troglodytes*
21 19 *verus*): evidence for empathy?. *Journal of Ethology* **29**, 365–368.
22 20
23 21 PRUETZ, J., ONTL, K. B., CLEAVELAND, E., LINDSHIELD, S., MARSHACK, J. & WESSLING, E. G.
24 22 (2017). Intragroup lethal aggression in chimpanzees (*Pan troglodytes verus*): inferred killing of a
25 23 former alpha male at Fongoli, Senegal. *International Journal of Primatology* **38**, 31–57.
26 24
27 25 RAJPUROHIT L.S. (1997). Why do mothers carry the corpses of their infants in Hanuman langurs,
28 26 *Presbytis entellus*. *Journal of Nature and Conservation* **9**, 183–193.
29 27
30 28 RAMÍREZ-LLORENS, P., DI BITETTI, M. S., BALDOVINO, M. C. & JANSON, C. H. (2008).
31 29 Infanticide in black capuchin monkeys (*Cebus apella nigrinus*) in Iguazu National Park,
32 30 Argentina. *American Journal of Primatology* **70**, 473–484.
33 31
34 32 REICHENOW, E. (1920). Biologische Beobachtungen an Gorilla und Schimpanse.
35 33 *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*. 1–40. (in German).
36 34
37 35 REN, B., LI, D., HE, X., QIU, J. & LI, M. (2011). Female resistance to invading males increases
38 36 infanticide in langurs. *Plos One* **6**, e18971.
39 37
40 38 REYNOLDS, V. (2005). *The chimpanzees of the Budongo forest: Ecology, behaviour and*
41 39 *conservation*. Oxford University Press, Oxford.
42 40
43 41 RILEY, C. M., KOENIG, B. L. & GUMERS, M. D. (2015). Observation of a fatal dog attack on a
44 42 juvenile long-tailed macaque in a human-modified environment in Singapore. *Nature in*
45 43 *Singapore* **8**, 57–63.
46 44
47 45 RIMBACH, R., PARDO-MARTINEZ, A., MONTES-ROJAS, A., DI FIORE, A. & LINK, A. (2012).
48 46 Interspecific Infanticide and Infant - Directed Aggression by Spider Monkeys (*Ateles hybridus*)
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 1 in a Fragmented Forest in Colombia. *American Journal of Primatology* **74**, 990–997.
4 2
5 3 ROBBINS, M. M., ANDO, C., FAWCETT, K. A., GRUETER, C. C., HEDWIG, D., IWATA, Y., LODWICK,
6 4 J. L., MASI, S., SALMI, R., STOINSKI, T. S., TODD, A., VECELLIO, V., YAMAGIWA, J. (2016).
7 5 Behavioral variation in gorillas: Evidence of potential cultural traits. *PLoS One* **11**, e0160483.
8 6
9 7 ROCHAT, M. J., SERRA, E., FADIGA, L. & GALLESE, V. (2008). The evolution of social cognition:
10 8 Goal familiarity shapes monkeys' action understanding. *Current Biology* **18**, 227–232.
11 9
12 10 RODA, S. A. & PONTES, A. R. M. (1998). Polygyny and infanticide in common marmosets in a
13 11 fragment of the Atlantic forest of Brazil. *Folia Primatologica* **69**, 372–376.
14 12
15 13 ROSATI, A. G., ARRE, A. M., PLATT, M. L. & SANTOS, L. R. (2016). Rhesus monkeys show
16 14 human-like changes in gaze following across the lifespan. *Proceedings of the Royal Society B:*
17 15 *Biological Sciences* **283**, 20160376.
18 16
19 17 ROSEN, J. B. & DONLEY, M. P. (2006). Animal studies of amygdala function in fear and
20 18 uncertainty: relevance to human research. *Biological Psychology* **73**, 49–60.
21 19
22 20 ROSENBLUM, L. A. & YOUNGSTEIN, K. (1974). Developmental changes in compensatory dyadic
23 21 response in mother and infant monkeys. In *The Effect of the Infant on its Caregiver* (eds M.
24 22 LEWIS and L.A. ROSENBLUM), pp. 141–161. Wiley, New York.
25 23
26 24 ROSENSON, L. M. (1977). The response of some prosimian mothers to their own anesthetized
27 25 infants. *Primates* **18**, 579–588.
28 26
29 27 ROSSANO, M. J. (2015). The evolutionary emergence of costly rituals. *PaleoAnthropology* **2015**,
30 28 78–100.
31 29
32 30 RUDRAN, R. (1973). Adult male replacement in one-male troops of purple-faced langurs
33 31 (*Presbytis senex senex*) and its effect on population structure. *Folia Primatologica* **19**, 166–192.
34 32
35 33 RUMBAUGH, D. M. (1965). Maternal care in relation to infant behavior in the squirrel monkey.
36 34 *Psychological Reports* **16**, 171–176.
37 35
38 36 SABATER-PI, J., BERMEJO, M., ILLERA, G. & VEA, J. J. (1993). Behavior of bonobos (*Pan*
39 37 *paniscus*) following their capture of monkeys in Zaire. *International Journal of Primatology* **14**,
40 38 797–804.
41 39
42 40 SAFINA, C. (2015). *Beyond words: what animals think and feel*. Henry Hold & Co, New York.
43 41
44 42 SALA, N., PANTOJA-PÉREZ, A., ARSUAGA, J. L., PABLOS, A. & MARTÍNEZ, I. (2016). The Sima
45 43 de los Huesos Crania: Analysis of the cranial breakage patterns. *Journal of Archaeological*
46 44 *Science* **72**, 25–43.
47 45
48 46 SANTINI, L. (2012). Conflictual behavior in a lemur mother toward a dying infant. *Lemur News*
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 1 **16**, 26–27.
4 2
5 3 SANTOS, L. R. & HAUSER, M. D. (1999). How monkeys see the eyes: Cotton-top tamarins'
6 4 reaction to changes in visual attention and action. *Animal Cognition* **2**, 131–139.
7 5
8 6 SANTOS, L. R. & HAUSER, M. D. (2002). A non-human primate's understanding of solidity:
9 7 dissociations between seeing and acting. *Developmental Science* **5**, F1–F7
10 8
11 9 SAPOLSKY, R. M. (2016). Psychiatric distress in animals versus animal models of psychiatric
12 10 distress. *Nature Neuroscience* **19**, 1387–1389.
13 11
14 12 SARABIAN, C. & MACINTOSH A. J. (2016) Revulsion in chimpanzees: health maintenance
15 13 through avoidance of biological contaminants. *PeerJ* (preprint).
16 14
17 15 SCHALLER, G. B. (1963). *The mountain gorilla*. University of Chicago Press, Chicago
18 16
19 17 SCHALLER, G. B. (1964). *The Year of the Gorilla*. Chicago: University of Chicago Press,
20 18 Chicago.
21 19
22 20 SCHMIDT, M. (2011). Locomotion and postural behaviour. *Advances in Science and Research* **5**,
23 21 23–39.
24 22
25 23 SCHOOF, V. A., WIKBERG, E. C., JACK, K. M., FEDIGAN, L. M., ZIEGLER, T. E. & KAWAMURA,
26 24 S. (2014). Infanticides during periods of social stability: Kinship, resumption of ovarian cycling,
27 25 and mating access in white-faced capuchins (*Cebus capucinus*). *Neotropical Primates* **21**, 191–
28 26 195.
29 27
30 28 SEAY, B., HANSEN, E. & HARLOW, H. F. (1962). Mother-infant separation in monkeys. *Journal*
31 29 *of Child Psychology and Psychiatry* **3**, 123–132.
32 30
33 31 SEMPLE, S., HIGHAM, J. P., MACLARNON, A. M., ROSS, C. & LEHMANN, J. (2010). Comment on
34 32 pan thanatology. [http://www.cell.com/current-biology/comments/S0960-9822%2810%2900145-](http://www.cell.com/current-biology/comments/S0960-9822%2810%2900145-4)
35 33 4.
36 34
37 35 SEPT, J. (1998). Shadows on a changing landscape: comparing nesting patterns of hominids and
38 36 chimpanzees since their last common ancestor. *American Journal of Primatology* **46**, 85–101.
39 37
40 38 SEYFARTH, R. M. & CHENEY, D. L. (2013). Affiliation, empathy, and the origins of theory of
41 39 mind. *Proceedings of the National Academy of Sciences* **110**, 10349–10356.
42 40
43 41 SHARMA, G., BHARTI, S., CHENA, R. & RAJPUROHIT, L.S. (2011). Dead infant carrying in the
44 42 Hanuman langur (*Semnopithecus entellus*) around Jodhpur (Rajasthan). *Laboratory Primate*
45 43 *Newsletter* **50**, 1–5.
46 44
47 45 SHEAK, H. W. (1917). Disposition and intelligence of the chimpanzee. *Proceedings of the*
48 46 *Indiana Academy of Science* **27**, 301–310.
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3
4 1
5 2 SHEETS-JOHNSTONE, M. (1986). On the conceptual origin of death. *Philosophy and*
6 3 *Phenomenological Research* **47**, 31–58.
7 4
8 5 SHOPLAND, J. M. & ALTMANN, J. (1987). Fatal intragroup kidnapping in yellow baboons.
9 6 *American Journal of Primatology* **13**, 61–65.
10 7
11 8 SHUMAKER, R. W., WALKUP, K. R. & BECK, B. B. (2011). *Animal tool behavior: the use and*
12 9 *manufacture of tools by animals*. John Hopkins University Press, Maryland.
13 10
14 11 SIMPSON, E. A., MILLER, G. M., FERRARI, P. F., SUOMI, S. J. & PAUKNER, A. (2016). Neonatal
15 12 imitation and early social experience predict gaze following abilities in infant monkeys.
16 13 *Scientific Reports* **6**, 20233.
17 14
18 15 SLAUGHTER, V. (2005). Young children’s understanding of death. *Australian Psychologist* **40**,
19 16 179–186.
20 17
21 18 SLAUGHTER, V., JAAKKOLA, K. & CAREY, S. (1999). Constructing a coherent theory: Children’s
22 19 biological understanding of life and death. In *Children’s understanding of biology, health and*
23 20 *ethics* (eds M. SEIGAL & C. PETERSON), pp. 71–98. Cambridge University Press, Cambridge.
24 21
25 22 SLIWA, J. & FREIWALD, W. A. (2017). A dedicated network for social interaction processing in
26 23 the primate brain. *Science* **356**, 745–749.
27 24
28 25 SMAERS, J. B., GÓMEZ-ROBLES, A., PARKS, A. N. & SHERWOOD, C. C. (2017). Exceptional
29 26 evolutionary expansion of prefrontal cortex in great apes and humans. *Current Biology* **27**, 714–
30 27 720.
31 28
32 29 SMUTS, B. B. (1985). *Sex and friendship in baboons*. Transaction Publishers, New York.
33 30
34 31 SOLTIS, J., THOMSEN, R., MATSUBAYASHI, K. & TAKENAKA, O. (2000). Infanticide by resident
35 32 males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behavioral*
36 33 *Ecology and Sociobiology* **48**, 195–202.
37 34
38 35 SOMMER, V. (1987). Infanticide among free-ranging langurs (*Presbytis entellus*) at Jodhpur
39 36 (Rajasthan/India): recent observations and a reconsideration of hypotheses. *Primates* **28**, 163–
40 37 197.
41 38
42 39 SPEECE, M. & BRENT, S. (1996). The development of children’s understanding of death. In
43 40 *Handbook of childhood death and bereavement* (eds C. CORR & D. CORR.), pp. 29–50. Springer,
44 41 New York.
45 42
46 43 SPEEDE, S. (2013). *Kindred beings: what seventy-three chimpanzees taught me about life, love,*
47 44 *and connection*. HarperOne, San Francisco.
48 45
49 46 SPELKE, E., PHILLIPS, A. & WOODWARD, A. (1995). Infants ‘ knowledge of object motion and

- 1
2
3 1 human action. In *Causal cognition: A multidisciplinary debate*. (eds D. SPERBER, D. PREMACK
4 2 and A. J. PREMACK), pp. 44–78. Clarendon Press, New York.
5 3
6 4 SPELKE, E. S. & KINZLER, K. D. (2007). Core knowledge. *Developmental Science* **10**, 89–96.
7 5
8 6 SPENCER-BOOTH, Y. & HINDE, R. A. (1971). Effects of 6 days separation from mother on 18-to
9 7 32-week-old rhesus monkeys. *Animal Behaviour* **19**, 174–191.
10 8
11 9 STEVENS, M. & MERILAITA, S. (2009). Animal camouflage: current issues and new perspectives.
12 10 *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **364**, 423–427.
13 11
14 12 STEWART, F. A., PIEL, A. K. & O'MALLEY, R. C. (2012). Responses of chimpanzees to a
15 13 recently dead community member at Gombe National Park, Tanzania. *American Journal of*
16 14 *Primatology* **74**, 1–7.
17 15
18 16 STINER, M. C. (2017). Love and death in the stone age: what constitutes first evidence of
19 17 mortuary treatment of the human body?. *Biological Theory* **12**, 248–261.
20 18
21 19 STRIER, K. B. (1996). Reproductive Ecology of Female Muriquis (*Brachyteles arachnoides*). In
22 20 *Adaptive Radiations of Neotropical Primates*. (eds M. A. NORCONK, A. L. ROSENBERGER & P.
23 21 A. GARBER), pp. 511–532. Plenum Press, New York.
24 22
25 23 STRUHSAKER, T. T. (1971). Social behaviour of mother and infant vervet monkeys
26 24 (*Cercopithecus aethiops*). *Animal Behaviour* **19**, 233–250.
27 25
28 26 STRUHSAKER, T. T. (1977). Infanticide and social organization in the redtail monkey
29 27 (*Cercopithecus ascanius schmidti*) in the Kibale forest, Uganda. *Zeitschrift für Tierpsychologie*
30 28 **45**, 75–84.
31 29
32 30 STRUHSAKER, T. T. (2010). *The red colobus monkeys: variation in demography, behavior, and*
33 31 *ecology of endangered species*. Oxford University Press, Oxford.
34 32
35 33 STRUHSAKER, T. T. & LELAND, L. (1985). Infanticide in a patrilineal society of red colobus
36 34 monkeys. *Zeitschrift für Tierpsychologie* **69**, 89–132.
37 35
38 36 STRUM, S. C. (1983). Baboon cues for eating meat. *Journal of Human Evolution* **12**, 327–336.
39 37
40 38 STRUM, S. C. (1987). *Almost human: a journey into the world of baboons*. University of Chicago
41 39 Press, Chicago.
42 40
43 41 SUGIYAMA, Y. (1967). Social organization of Hanuman langurs. In *Social communication among*
44 42 *primates* (ed. S.E. Altmann), pp.41–72. University of Chicago Press, Chicago
45 43
46 44 SUGIYAMA, Y., KURITA, H., MATSUI, T., KIMOTO, S. & SHIMOMURA, T. (2009). Carrying of
47 45 dead infants by Japanese macaque (*Macaca fuscata*) mothers. *Anthropological Science* **117**,
48 46 113–119.
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3
4 1
5 2 SUWA, G., ASFAW, B., KONO, R. T., KUBO, D., LOVEJOY, C. O. & WHITE, T. D. (2009). The
6 3 *Ardipithecus ramidus* skull and its implications for hominid origins. *Science* **326**, 68–68e7.
7 4
8 5 SWEDELL, L. & TEFAYE, T. (2003). Infant mortality after takeovers in wild Ethiopian
9 6 hamadryas baboons. *American Journal of Primatology* **60**, 113–118.
10 7
11 8 TAYLOR, H., TEAS, J., RICHIE, T., SOUTHWICK, C. & SHRESTHA, R. (1978). Social interactions
12 9 between adult male and infant rhesus monkeys in Nepal. *Primates* **19**, 343–351.
13 10
14 11 TEICHROEB, J. A. & SICOTTE, P. (2008). Infanticide in ursine colobus monkeys (*Colobus*
15 12 *vellerosus*) in Ghana: new cases and a test of the existing hypotheses. *Behaviour* **145**, 727–755.
16 13
17 14 TELEKI, G. (1973). Group response to the accidental death of a chimpanzee in Gombe National
18 15 Park, Tanzania. *Folia Primatologica* **20**, 81–94.
19 16
20 17 THOMPSON, C. L., HRIT, R. T., VINYARD, C. J., BOTTENBERG, K. N. & DE OLIVEIRA, M. A.
21 18 (2018, August). Behavioral responses of a wild common marmoset (*Callithrix jacchus*) group
22 19 toward an infant's death at Tapacurá Field Station, Pernambuco, Brazil. Lecture presented at the
23 20 27th Congress of International Primatological Society.
24 21
25 22 THOMPSON, S. (2009). *The intimate ape, orangutans and the secret life of a vanishing species*.
26 23 Citadel Press, New York.
27 24
28 25 THOMPSON, R. K., FLEMMING, T. M. & HAGMANN, C. E. (2016). Can old-world and new-world
29 26 monkeys judge spatial above/below relations to be the same or different? Some of them, but not
30 27 all of them. *Behavioural Processes* **123**, 74–83.
31 28
32 29 TIAN, J., ZHANG, S., GUO, Y., GARBER, P. A., GUO, W. & LU, J. (2016). Evidence of
33 30 placentophagia and mother-infant cannibalism in free-ranging *Macaca mulatta tcheliensis* in
34 31 Mount Taihangshan, Jiyuan, China. *Folia Primatologica* **87**, 381–391.
35 32
36 33 TODA, K., TOKUYAMA, N. & FURUICHI, T. (2017). An Old Female Bonobo Carried a Dead Red-
37 34 Tailed Monkey for over a Month. *Pan Africa News* **24**, 19–21.
38 35
39 36 TOKUYAMA, N., EMIKEY, B., BAFIKE, B., ISOLUMBO, B., IYOKANGO, B., MULAVWA, M. N. &
40 37 FURUICHI, T. (2012). Bonobos apparently search for a lost member injured by a snare. *Primates*
41 38 **53**, 215–219.
42 39
43 40 TOKUYAMA, N., MOORE, D. L., GRAHAM, K. E., LOKASOLA, A. & FURUICHI, T. (2017). Cases of
44 41 maternal cannibalism in wild bonobos (*Pan paniscus*) from two different field sites, Wamba and
45 42 Kokolopori, Democratic Republic of the Congo. *Primates* **58**, 7–12.
46 43
47 44 TOMASELLO, M. & CARPENTER, M. (2007). Shared intentionality. *Developmental Science* **10**,
48 45 121–125.
49 46
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 1 TOOTH, N. & SCHICK, K. (2018). An overview of the cognitive implications of the Oldowan
4 2 Industrial Complex. *Azania: Archaeological Research in Africa* **53**, 3–39.
5 3
6 4 TREVARTHEN, C. (1977). Descriptive analysis of infant communicative behavior. In *Studies in*
7 5 *mother-infant interaction* (ed H. R. Schajfer), pp. 227–270. Academic Press, London.
8 6
9 7 TROJE, N. F. & WESTHOFF, C. (2006). The inversion effect in biological motion perception:
10 8 Evidence for a “life detector”?. *Current Biology* **16**, 821–824.
11 9
12 10 TURCKHEIM G. & MERZ, E. (1984). Breeding Barbary macaques in outdoor open enclosures. In
13 11 *The Barbary Macaque: A Case Study in Conservation*. (ed J.E. Fa), pp 241–261. Plenum Press,
14 12 London.
15 13
16 14 TURNER S.E., GOULD L. & DUFFUS D.A. (2005). Maternal behavior and infant congenital limb
17 15 malformation in a free-ranging group of *Macaca fuscata* on Awaji Island, Japan. *International*
18 16 *Journal of Primatology* **26**, 1435–1457.
19 17
20 18 ULLER, C. (2004). Disposition to recognize goals in infant chimpanzees. *Animal Cognition* **7**,
21 19 154–161.
22 20
23 21 VALDERRAMA, X., SRIKOSAMATARA, S. & ROBINSON, J. G. (1990). Infanticide in wedge-capped
24 22 capuchin monkeys, *Cebus olivaceus*. *Folia Primatologica* **54**, 171–176.
25 23
26 24 VALLORTIGARA, G. & REGOLIN, L. (2006). Gravity bias in the interpretation of biological motion
27 25 by inexperienced chicks. *Current Biology* **16**, R279–R280.
28 26
29 27 VAN BELLE, S., KULP, A., THIESSEN-BOCK, R., GARCIA, M. & ESTRADA, A. (2010). Observed
30 28 infanticides following a male immigration event in black howler monkeys, *Alouatta pigra*, at
31 29 Palenque National Park, Mexico. *Primates* **51**, 279–284.
32 30
33 31 VAN LAWICK-GOODALL, J. (1968). The behaviour of free-living chimpanzees in the Gombe
34 32 Stream Reserve. *Animal Behaviour Monographs* **1**, 161–311.
35 33
36 34 VAN LAWICK-GOODALL, J. (1971). *In the shadow of man*. Houghton Mifflin Harcourt, London.
37 35
38 36 VAN LEEUWEN, E. J., MULENGA, I. C., BODAMER, M. D. & CRONIN, K. A. (2016). Chimpanzees’
39 37 responses to the dead body of a 9-year-old group member. *American Journal of Primatology* **78**,
40 38 914–922.
41 39
42 40 VAN LEEUWEN, E. J., CRONIN, K. A. & HAUN, D. B. (2017). Tool use for corpse cleaning in
43 41 chimpanzees. *Scientific Reports* **7**, 44091.
44 42
45 43 VECELLIO, V. (2009). Juvenile in titus group dead. Retrieved from
46 44 <https://gorillafund.org/juvenile-in-titus-group-dead/>
47 45
48 46 VIEIRA, A. B. (1987). Níveis de consciência da morte nos primatas: uma leitura piagetiana.
49 57
50 58
51 59
52 60

- 1
2
3 1 *Psicologia* **5**, 167–176. (in Portuguese).
4 2
5 3 VONK, J. (2003). Gorilla (*Gorilla gorilla gorilla*) and orangutan (*Pongo abelii*) understanding of
6 4 first- and second-order relations. *Animal Cognition* **6**, 77–86.
7 5
8 6 WARREN, Y. & WILLIAMSON, E. A. (2004). Transport of dead infant Mountain gorillas by
9 7 mothers and unrelated Females. *Zoo Biology* **23**, 375–378.
10 8
11 9 WATSON, C., HASHIMOTO, N., TAKAYOSHI, N., OKAMOTO, N. & MATSUZAWA, T. (2015). Two
12 10 cases of dead infant carrying followed by mother infant cannibalism in captive socially housed
13 11 Japanese macaques. *Folia Primatologica* **86**, 378–379.
14 12
15 13 WATSON, C. F. & MATSUZAWA, T. (2018). Behaviour of nonhuman primate mothers toward
16 14 their dead infants: uncovering mechanisms. *Philosophical Transactions of the Royal Society B:
17 15 Biological Sciences* **373**, 20170261.
18 16
19 17 WATTS D. & HESS J. (1988). Twin birth in wild mountain gorillas. *Oryx* **22**, 5–6.
20 18
21 19 WATTS, D. P. & MITANI, J. C. (2000). Infanticide and cannibalism by male chimpanzees at
22 20 Ngogo, Kibale National Park, Uganda. *Primates* **41**, 357–365.
23 21
24 22 WATTS, D. P. (2008). Scavenging by chimpanzees at Ngogo and the relevance of chimpanzee
25 23 scavenging to early hominin behavioral ecology. *Journal of Human Evolution* **54**, 125–133.
26 24
27 25 WEINGRILL, T. (2000). Infanticide and the value of male-female relationships in mountain
28 26 chacma baboons. *Behaviour* **137**, 337–359.
29 27
30 28 WESTOLL, A. (2011). *The chimps of Fauna Sanctuary: A true story of resilience and recovery*.
31 29 Houghton Mifflin Harcourt, New York.
32 30
33 31 WHALEN, P. J. (2007). The uncertainty of it all. *Trends in Cognitive Sciences* **11**, 499–500.
34 32
35 33 WHILDE, J. & MARPLES, N. (2011). The behavior of a zoo-housed infant orangutan after the
36 34 death of its mother. *Zoo Biology* **30**, 205–211.
37 35
38 36 WHITE, C., MARIN, M. & FESSLER, D. M. (2017). Not just dead meat: An evolutionary account
39 37 of corpse treatment in mortuary rituals. *Journal of Cognition and Culture* **17**, 146–168.
40 38
41 39 WINEGARD, B. M., REYNOLDS, T., BAUMEISTER, R. F., WINEGARD, B. & MANER, J. K. (2014).
42 40 Grief functions as an honest indicator of commitment. *Personality and Social Psychology
43 41 Review* **18**, 168–186.
44 42
45 43 WISMAN, A. & SHRIRA, I. (2015). The smell of death: evidence that putrescine elicits threat
46 44 management mechanisms. *Frontiers in Psychology* **6**, 1274.
47 45
48 46 WOODWARD, A. L. (1998). Infants selectively encode the goal object of an actor's reach.
49 50
50 51
51 52
52 53
53 54
54 55
55 56
56 57
57 58
58 59
59 60
60

1
2
3 1 *Cognition* **69**, 1–34.

4 2
5 3 WOODWARD, A. L., SOMMERVILLE, J. A. & GUAJARDO, J. J. (2001). How infants make sense of
6 4 intentional action. In *Intentions and intentionality: Foundations of social cognition*. (eds B. F.
7 5 MALLE, L. J. MOSES & D. A. BALDWIN), pp. 149–71. MIT Press, Massachusetts.

8 6
9 7 WRANGHAM, R. & OTALI, E. (2011) Teddy's death and the aftermath. Retrieved from:
10 8 <https://kibalechimpanzees.wordpress.com/2011/06/23/teddys-death-and-the-aftermath/>

11 9
12 10 WROBLEWSKI, E. E. (2008). An unusual incident of adoption in a wild chimpanzee (*Pan*
13 11 *trogodytes*) population at Gombe National Park. *American Journal of Primatology* **70**, 995–998.

14 12
15 13 YAMAGIWA, J. & KAHEKWA, J. (2004). First observations of infanticides by a silverback in
16 14 Kahuzi-Biega. *Gorilla Journal* **29**, 6–9.

17 15
18 16 YANG, B., ANDERSON, J. R. & LI, B. (2016). Tending a dying adult in a wild multi-level primate
19 17 society. *Current Biology* **26**, R387–R407.

20 18
21 19 YAO, H., YU, H., YANG, B., YANG, W., XU, H., GRUETER, C. C., LI, M. & XIANG, Z. (2016).
22 20 Male Infanticide in the Golden Snub-Nosed Monkey (*Rhinopithecus roxellana*), a Seasonally
23 21 Breeding Primate. *International Journal of Primatology* **37**, 175–184.

24 22
25 23 YERKES, R. M. (1915). Maternal instinct in a monkey. *Journal of Animal Behavior* **5**, 403–405.

26 24
27 25 YERKES, R. M. & YERKES A. W. (1929). *The great apes: a study in anthropoid life*. Yale
28 26 University Press, New Haven.

29 27
30 28 YOSHIDA, H. (1994). A case report about the death accident of captive chimpanzee infant.
31 29 *Primate Research* **10**, 321–331. (Japanese with English Summary).

32 30
33 31 ZAMMA, K. (2002). A chimpanzee trifling with a squirrel: pleasure derived from teasing. *Pan*
34 32 *Africa News* **9**, 9–11.

35 33
36 34 ZELLER, A. (1991). The grieving process in non-human primates. In *Coping with the final*
37 35 *tragedy: cultural variation in dying and grieving*. (eds D.R. Counts and D.A. Counts), pp. 5–26.
38 36 Baywood Publishing Company Inc, Amityville, NY.

39 37
40 38 ZUCKERMAN, S. (1932). *The social life of monkeys and apes*. Kegan Paul, Trench, Trubner & Co,
41 39 London.

42 40

43 41 **VIII. SUPPORTING INFORMATION**

44 42 Additional supporting information may be found in the online version of this article

45 43 **Appendix S1.** Dead-infant carrying across non-human primates.

46 44 **Appendix S2.** Responses to dead/dying infants in strepsirrhines and callithrichines.

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- 1 **Appendix S3.** Infant abandonment during violent deaths in non-human primates.
 - 2 **Appendix S4.** Responses to dead juveniles and adults in non-human primates.

For Review Only

1 **Figure legends**

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

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

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

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

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

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

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

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

1 Table 1. Dead-infant carrying hypotheses.
2

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

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	carrying the infants again (Pollock, 1961; Hamburg, 1972).
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For Review Only

1 Table 2. Conceptual acquisition of death in humans¹.

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

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

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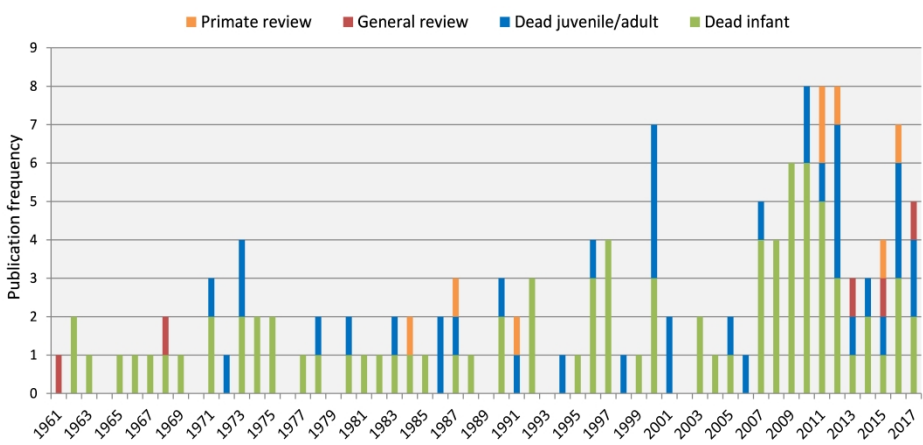


Figure 1. Publication frequency on the subject of primate thanatology from 1961 to 2017. The search was conducted in www.scholar.google.com using keywords: "dead"/"deceased" + "infant"/"conspecific" and the corresponding genus (i.e. *Macaca*, *Pan*).



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

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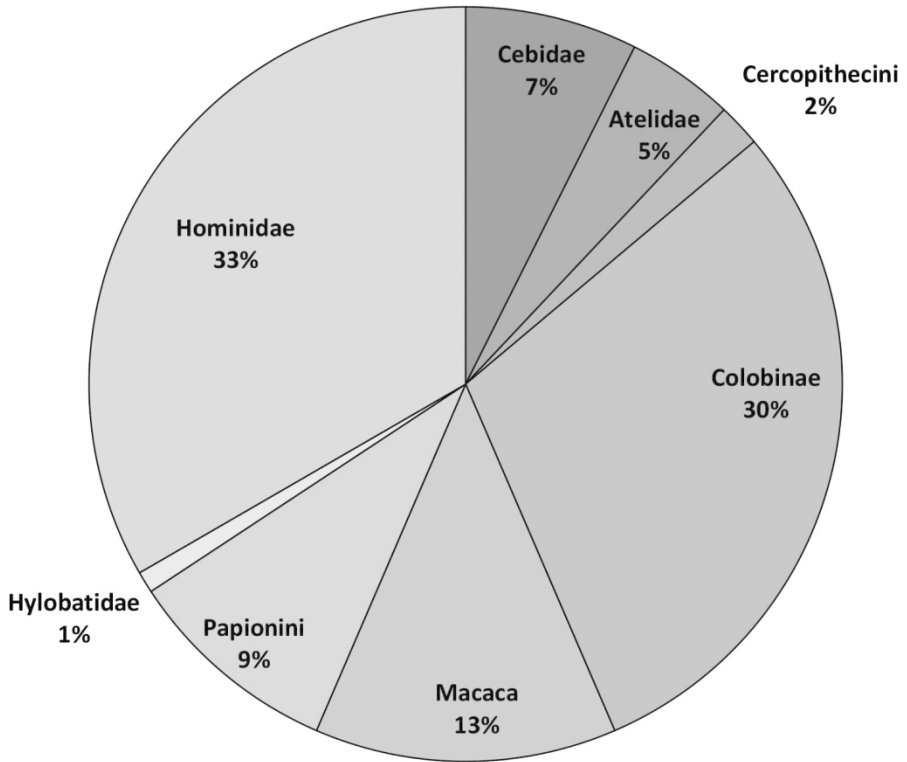


Figure 3. Dead-infant carrying behaviour distribution across primate taxa collected from single case reports (N = 110). Note: Papionini refers only to *Papio* and *Theropitecus* genera. See Appendix S1 for further details.



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

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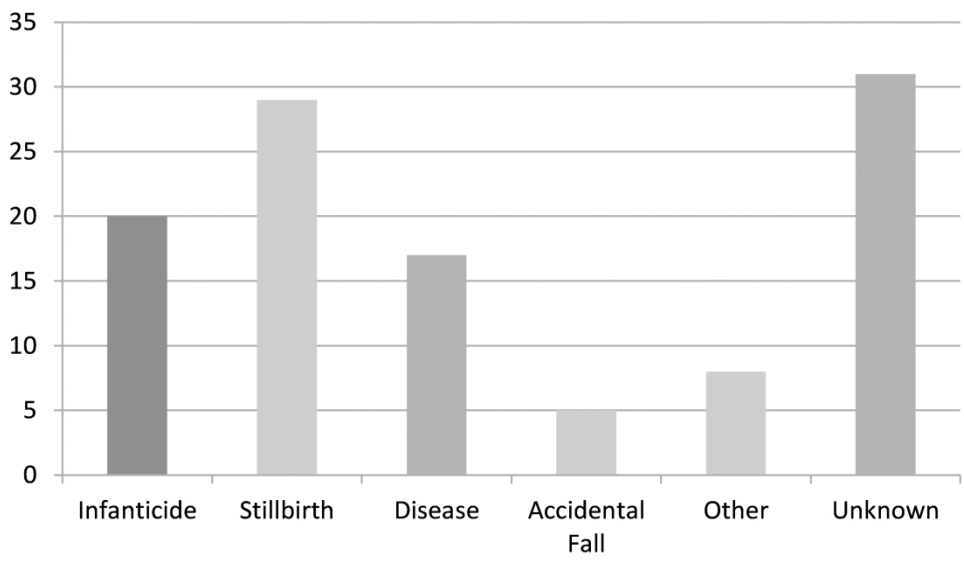


Figure 5. Cause of death in cases of dead-infant carrying collected from single case reports (N = 110). See Appendix S1 for further details.



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

352x236mm (72 x 72 DPI)

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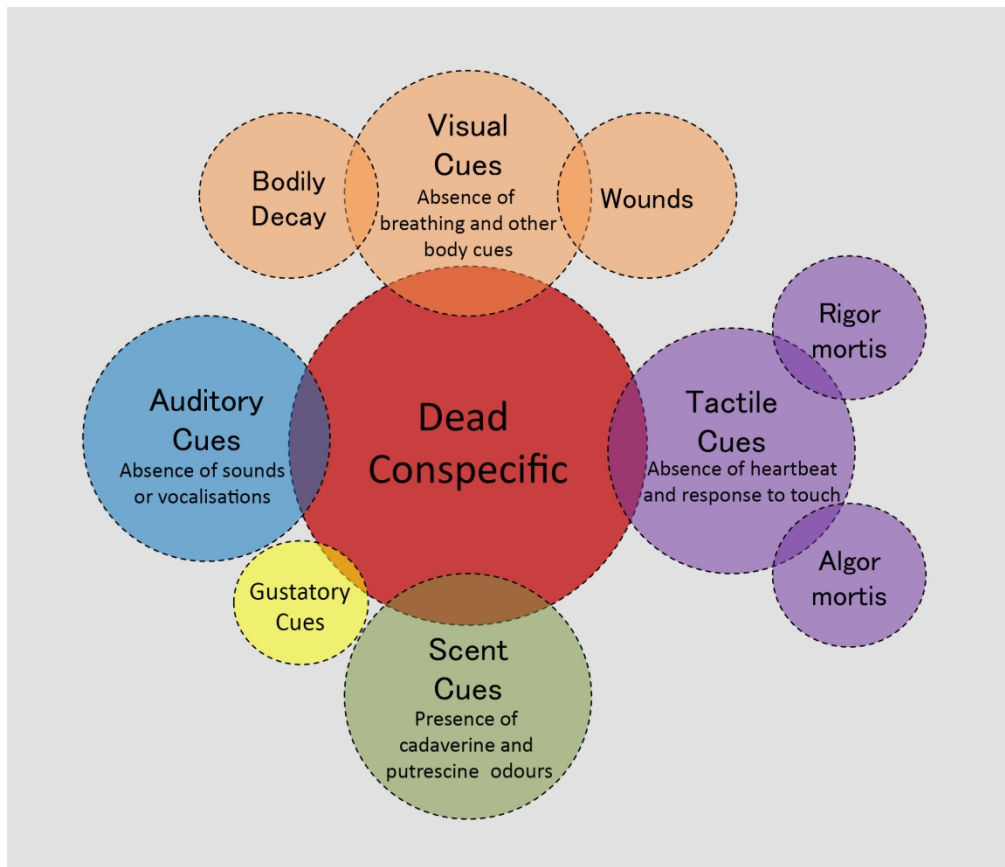
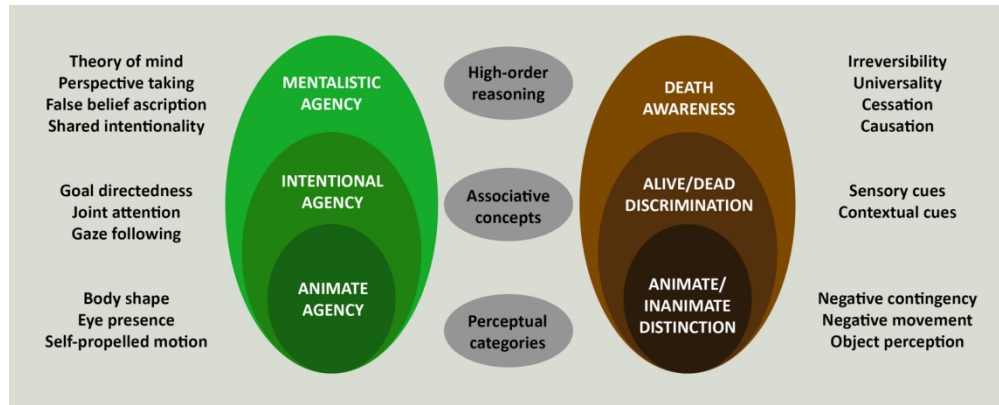


Figure 7. Sensory cues to death available to primates: a combination of the presence and absence of signals.



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

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

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

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

1. Schoof, V. A., et al. (2014). 2. Perry, S. & Manson, J. H. (2009). 3. Valderrama, X., et al. (1990). 4. Izar, et al. (2007). 5. Ramirez-Llorens, P. et al (2008). 6. Izawa, K. (1992). 7. Rumbaugh, D. M. (1965). 8. Strier, K. B. (1996). 9. Possamai, C. B., et al (2007). 10. Iurck, M. F., et al (2005). 11. Gibson, K. N., et al. (2008). 12. Beltrán, M. L. & Stevenson, P. R. (2012).

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

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

1. Nash, L. T. (1974). 2. Weingrill, T. (2000). 3. Shopland, J. M. & Altmann, J. (1987). 4. Pereira, M. E. (1983). 5. Markham, A. C., et al. (2011). 6. Markham, A. C. (pers. comm.). 7. Swedell, L. & Tesfaye, T. (2003). 8. Bernstein, I. S. (1975). 9. Mori, A., et al. (2003). 10. Mori, A., et al. (1997). 11. Lu, J.Q., et al. (2007). 12. Guo, D., et al. (2016). 13. Li, T., et al. (2012). 14. Yao, H., et al. (2016). 15. Teichroeb, J. A. & Scotte, P. (2008). 16. Bernstein, I. S. & Sharpe, L. G. (1966). 17. Ciani, A. C. (1984). 18. Chai, W., et al. (2013). 19. Balasubramanian, M. & Sabu-Jahas, S. A. (1997). 20. Das, S., et al. (2018). 21. Chen, R. & Li, K. (2011). 22. Hsiang-Jen, S. & Hsiu-Hui, S. (2008). 23. Watson, C., et al. (2015). 24. De Marco, A., et al. (2017). 25. Gupta, A. K. (2000). 26. Nakagawa, N. (2007). 27. McKenna, J. J. (1982).

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

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

1. Rajpurohit L.S. (1997). 2. Sharma *et al.* (2011).

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

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

1. Palombit, R. A. (1995). 2. Dellatore, D. F. *et al.* (2009). 3. Schaller, G. B. (1963). 4. Fossey, D. (1984). 5. Watts D. & Hess J. (1988). 6. Fossey, D. (1983). 7. Warren, Y. & Williamson, E. A. (2004). 8. Yamagiwa, J. & Kahekwa, J. (2004). 9. Kano, T. (1992). 10. Fowler, A. & Hohmann, G. (2010). 11. van Lawick-Goodall, J. (1968). 12. Goodall, J. (1977). 13. Wroblewski, E. E. (2008). 14. Boesch, C. & Boesch-Achermann, H. (2000). 15. Boesch, C. (2012). 16. Boesch, C. (pers. comm.). 17. Matsuzawa, T. (1997). 18. Biro, D. *et al.* (2010). 19. Cronin, K. A. *et al.* (2011). 20. Nishida, T. (1973). 21. Nishida, T. (1981). 22. Nishida, T. (1998). 23. Hosaka, K. *et al.* (2000). 24. Hanamura, S. *et al.* (2008). 25. Kooriyama, T. (2009).

*Case not counted as infanticide.

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

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

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

1. Littlefield, B. L. (2010). 2. Santini, L. (2012). 3. Nakamichi, M., *et al.* (1996).

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

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

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

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

Table S3.1. Infant abandonment during violent deaths

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

1. Valderrama, X., et al. (1990). 2. Schoof, V. A., et al. (2014). 3. Agoramoorthy, G. & Rudran, R. (1995). 4. Van Belle, S., et al. (2010). 5. García-Feria, L. M., et al. (2015). 6. Clarke, M. R. (1983). 7. Gibson, K. N., et al. (2008). 8. Rimbach, R., et al. (2012). 9. Alvarez, S., et al. (2015). 10. Böer, M. & Sommer, V. (1992). 11. Fairgrieve, C. (1995). 12. Cords, M. & Fuller, J. L. (2010). 13. Struhsaker, T. T. (1977). 14. Struhsaker, T. T. & Leland, L. (1985). 15. Onderdonk, D. A. (2000). 16. Teichroeb, J. A. & Sicotte, P. (2008). 17. Agoramoorthy, G., & Mohnot, S. M. (1988). 18. Sommer, V. (1987). 19. Newton, P. N. (1986). 20. Ren, B., et al. (2011). 21. Soltis, J., et al. (2000). 22. Alfred, J. R. B. & Sati, J. P. (1991). 23. Fossey, D. (1984). 24. Goodall, J. (1977). 25. Newton-Fisher, N. E. (1999). 26. Watts, D. P., & Mitani, J. C. (2000). 27. Das, S., et al. (2018). 28. Matsuda, I., et al. (2008).

*Case not included in section III.1e

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

Table S4.1. Responses to dead juveniles and adults

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

References: 1. Stewart, F. A., et al. (2012). 2. Teleki, G. (1973). 3. Anderson, J. R., et al. (2010). 4. Westoll, A. (2011). 5. Bekoff, M. (2010). 6. Boesch, C. (2012). 7. Boesch & Boesch Achermann (2000). 8. Fawcett, K. & Muhuzuma, G. (2000). 9. van Leeuwen, E. J., et al. (2016). 10. Pruetz, J., et al. (2017). 11. Wrangham, R. & Otali, E. (2011). 12. Hofer, A., et al. (2000). 13. Fossey, D. (1983). 14. Prince-Hughes, D. (2001). 15. King, B. J. (2013). 16. Strum, S. C. (1987). 17. Buhl, J. S., et al. (2012). 18. Campbell, L. A. D., et al. (2016). 19. Gupta, A. K. (2000). 20. Yang, B., et al. (2016). 21. Bezerra, B. M., et al. (2014). 22. Safina, C. (2015).

Review Only