

1 **COMPARATIVE THANATOLOGY, AN INTEGRATIVE APPROACH: EXPLORING**
2 **SENSORY/COGNITIVE ASPECTS OF DEATH RECOGNITION IN VERTEBRATES**
3 **AND INVERTEBRATES**

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Abstract

Evolutionary thanatology benefits from broad taxonomic comparisons of non-human animals' responses to death. Furthermore, exploring the sensory and cognitive bases of these responses promises to allow classification of the underlying mechanisms on a spectrum from phylogenetically ancient to more derived traits. We draw on studies of perception and cognition in invertebrate and vertebrate taxa (with a focus on arthropods, corvids, proboscids, cetaceans and primates) to explore the cues that these animals use to detect life and death in others, and discuss proximate and ultimate drivers behind their capacities to do so. Parallels in thanatological behaviour exhibited by the last four taxa suggest similar sensory-cognitive processing rules for dealing with corpses, the evolution of which may have been driven by complex social environments. Uniting these responses is a phenomenon we term "animacy detection malfunction", whereupon the corpse, having both animate and inanimate attributes, creates states of fear/curiosity manifested as approach/avoidance behaviours in observers. We suggest that integrating diverse lines of evidence (including the "uncanny valley" effect originating from the field of robotics) provides a promising way to advance the field, and conclude by proposing avenues for future research.

Keywords: sensory cues, animacy, agency, uncanny corpse, death detection mechanism

1. INTRODUCTION

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

(Darwin, 1871, p.73) [1]

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

(Griffin, 1976, p.104-105) [2]

Awareness of death has been regarded as one of the defining traits of *Homo sapiens* by distinct schools of thought including philosophy [3], psychology [4], anthropology [5] and biology [6]. However, at least since Charles Darwin the possibility of a psychological continuity between humans and other animals has been entertained. While Darwin himself expressed doubts regarding the extent to which non-human animals (hereafter: "animals") could comprehend the death of a conspecific, his question was of a different nature than that of Griffin (see quotes above): he asked not if animals have an awareness of their own mortality, but, more modestly, to what extent they recognize death in others and how they "felt" in response.

These questions are at the centre of the field of Comparative Thanatology [7], which is concerned with how animals respond to their dead. Recent scientific interest notwithstanding, so-called funerary activities among animals have been reported since ancient times. Most notably, stories of elephants and ants burying their dead or dolphins assisting dead companions to the surface are recounted by Pliny the Elder (A.D. 29-79) and Aelian (A.D. 175-235) [8-9]. Already in the 18th and 19th centuries, first-hand reports and anecdotes accumulated on the interactions of animals with dead conspecifics. These included protection of the corpse, transport, vigils and emotional distress, with allusions to grief in non-human primates [10-11], corvids [12-13], proboscids [14-15], cetaceans [16], ungulates [17],

carnivores [18-19] and sirenians [20]. Observations similar to these have been confirmed more recently by researchers studying many of the same species [21-27].

In the present paper, our aim is to bring together hitherto partially disparate lines of research, which, in combination, can provide new perspectives on how, and to what extent, non-human animals detect death in others. We draw on empirical case reports as well as current research on animal perception and cognition relevant to elucidating some of their enigmatic responses towards their dead, compare these responses across taxa, and discuss how they may have emerged in the course of evolution. We begin by exploring how animals detect life, then through what cues they might detect death, and which aspects of cognition might contribute to processing such sensory information as “death awareness”. We conclude by proposing avenues for future research.

2. DETECTING LIFE

Within their natural surroundings, animals are constantly confronted with dynamic (moving) visual signals. Interpreting these correctly is a significant factor in evolutionary fitness, as such signals can come from both living (self-propelled motion patterns) or non-living (objects moved by external forces) entities [28]. The ability to distinguish biological from non-biological movement was presumably part of an ancient mechanism that evolved for modulating interactions with other organisms, be they heterospecific predators or prey, or conspecific kin, mates or competitors.

Movement through self-propelled motion was present in the first living organisms during the Pre-Cambrian some 3000 mya. These organisms moved around with the help of cilia and flagella [29]. Predation was already a strong selective force and one which likely gave rise to the first Eukaryotes [30] around 1600-2500 mya [31]. By the Ediacaran Period (700 mya) a division between chordates, mollusks and arthropods appeared, as indicated by genetic and fossil evidence [32]. These organisms were essentially relegated to a two-dimensional world confined by bio-mat grazing [33] where, possessing photo-receptors, they navigated discerning between light and darkness. Later yet, during the Cambrian Period, in an increasingly three dimensional world [34] innovations in many animals emerged that have

continued until now: the presence of brains and nervous systems [35], fully formed eyes [36], attention [37], associative learning [38], embodied cognition [39], and even the beginnings of primary consciousness [40].

Biological Motion. It was in the field of biological motion perception [77] that researchers found evidence for a perceptual life detector likely common to all land vertebrates [41]. Humans [42, 186] and newly hatched chicks [43] were presented with stimuli consisting of moving light point displays against a dark background, one set of stimuli depicting a moving being (human or other) and the other a moving but scrambled or inverted version of the first. Despite light points being severely impoverished percepts, the visual system decodes them in a straightforward manner when their movement corresponds to biological motion, but not non-biological motion; both studies found quick detection by humans and an inherent attraction in the chicks towards biological as opposed to non-biological motion. Further evidence for an ancient neural mechanism common for the detection of animacy came from additional studies with chicks [44] and with human newborns, who also attend preferentially to biological motion stimuli [45-46].

Recent work confirms the biological motion effect in adults of species such as Medaka fish [47], pigeons [48], rats [49], cats [50], dolphins [51], and non-human primates including common marmosets [52], rhesus monkeys [53], baboons [54] and chimpanzees [55]. But to date no newborn non-human primate has been tested, hence the issue of innateness is unresolved outside humans. The ability to detect biological movement paired with an inversion effect has some commonalities with other fields in perception such as face recognition in humans [56] and non-human primates [57], a capacity that appears to be innate in many species including primates [58]. The perception of biological motion is likely only one of many components of a larger perceptual system for animacy detection comprising "detectors" of biological cues such as faces, eyes, texture, odour and particular shapes, all fundamentally tied with agency attribution. In humans, self-propelled motion by itself is not a sufficient cue to trigger detection of intentional agency [59-60].

The Animate/Inanimate Distinction. In a recent review of the development of the animate-inanimate distinction in human infants, in addition to biological motion and self-propelled movement, Opfer and Gelman [61] list goal-directed movement (the directness with

which an agent moves towards its perceived goal) and contingency of behaviour (the timing between an agent's actions and specific events) as cues. In studies of human infants' capacity to decode an agent's intentions, infants seeing a human hand reaching for an object react to changes in its goals, whereas no such response is observed when a mechanical rod or claw replaces the hand [62-66]. Similar results have been found in capuchin monkeys (*Cebus apella*) [67], while the use of a monkey-like robot but not a moving box induces goal-direction ascription in common marmosets (*Callithrix jacchus*) [68]. During later development, these components of animacy attribution underlie various aspects of human infants' social cognition [76]. Importantly, the developing refinement of understanding and attribution errors are informative in terms of infants' categorisation of 'alive' vs 'dead' (including discrete components of full death-awareness: universality, irreversibility, causation and non-functionality [69], see also Anderson, this volume).

The animate and inanimate conceptual categories may relate to distinct neural circuits representing domain-specific knowledge systems that are evolutionarily adaptive [70-71]. Support for this theory includes discovery of a close match between humans and rhesus macaques (*Macaca mulatta*) in inferior temporal cortical object representations, both categorical and continuous [72-73].

3. DETECTING DEATH

3.1 Scent cues

In the animal kingdom, responses to dead conspecifics include necrophobia (avoidance), necrophagia (feeding) and necrophoresis (transport), and in many cases these are elicited primarily by chemical signals. Aversion to "death scents" (fatty acid necronomes or cadaverine/putrescine) may be a highly conserved response that is either innate or acquired easily due to a predisposition. Unlike freezing [74] or thanatosis (death-feigning) [75] which are visual in character, energetically non-costly and have evolved to transmit a specific message from sender to receiver, scent associated with decomposition is an unambiguous cue that receivers can reliably exploit. Necrophobic responses are adaptive in terms of

predator evasion or pathogen avoidance. Below we explore in more detail specifically scent-triggered responses to dead conspecifics across different taxa.

In eusocial insects (numerous species of ants, termites and bees), two major, non-mutually exclusive scent-based hypotheses have been proposed to explain the typical burial or corpse removal responses to dead colony members (reviewed in [25] and [77]; see also Sun et al., this issue). These hypotheses relate to the presence of specific chemical death-cues (“necromones”), and to the absence of chemical signatures of life (“chemical vital signs”), respectively. For example, while some ant species apparently respond to the decomposition-driven accumulation of fatty acids in corpses [78-79] others, such as the Argentine ant (*Linepithema humile*), engage in undertaking activities following the rapid disappearance upon death of cuticular chemicals secreted by live individuals [80]. As the latter mechanism potentially allows for a faster response, it is likely favoured in situations where the removal of dead bodies is time-sensitive, for example in densely populated colonies where the risk of contamination from pathogens is high. Interestingly, sensitivity to these cues appears to vary in some species according to caste – e.g. soldiers of *Atta mexicana* do not respond to oleic acid, the most common death cue in many social insects [81] – consistent with the observation that undertaking and corpse removal responses are often performed by a subset of colony members only, in a division of labour. Outside of eusocial insects, several genera of Isopoda as well as social caterpillars are known to be sensitive to oleic and linoleic acid extracts (and to avoid these chemical cues), suggesting an ancient origin stretching back to at least the Crustacea-Hexapoda common ancestor 420 mya, for the involvement of necromones in arthropod corpse removal behaviour [82].

In contrast, among vertebrates, death cues such as cadaverine and putrescine, alongside other decay- and putrefaction-related substances, typically elicit aversion responses. Zebrafish avoid cadaverine [83] and show elevated stress levels upon encounter [84], and sea lampreys [85] and sharks [86] avoid odours emanating from decaying conspecific tissue. Rodents, including various species of mice, voles, shrews and chipmunks also avoid areas where deceased rodents - even heterospecifics - are present, presumably at least partly informed by olfactory cues associated with decaying flesh [87]. California sea lions reportedly avoided a pool used for cooling after the carcass of a dead pup fell into it,

moving away after apparently sniffing at it [88]. In humans, a range of interesting emotional and conscious, and unconscious responses to putrescine have been documented, including increased vigilance, active and planned retreat, and hostility towards out-group members [89]. However, not all vertebrates show avoidance: in rats cadaverine and putrescine elicit the burying of dead conspecifics [90], and in goldfish the same chemicals enhance feeding activity [91].

3.2 Beyond scent: visual, tactile, multi-modal cues

Many animal species exhibit complex responses towards their dead that are not necessarily triggered by scent; furthermore, these often rely on a combination of several sensory modalities. Already among the arthropod examples described above, scent cues may combine with tactile cues to modulate responses to dead conspecifics (e.g. in the termite *Reticulitermes virginicus*; [92]), although the latter alone are insufficient to trigger a response. Here, we explore non-olfactory and multi-modal cue use in corvids, proboscids, cetaceans and primates, with a focus on observational and experimental field studies. The species comprising these taxa display many complex behaviours across both the physical and social domains, and have been argued to possess episodic-like memory. Many live in hierarchy-based social structures in which they cross-modally recognize individuals and act based on their past interactions [93-99]. Moreover, some individuals in these taxa are able to recognize themselves in the mirror, suggesting self-awareness [100-103]. It has been suggested that such species might be capable of an understanding of death [104]; however, there appears to be no qualitative difference between species that fail and those that pass the mirror test of self-recognition in regards to thanatological behaviour (i.e. dead infant carrying, exploratory behaviours towards the corpse, vigils, visitations, etc.) [105].

Corvids. The family Corvidae includes crows, ravens, rooks, magpies, jays and jackdaws. These species generally live in bonded pairs, possess the largest relative brain size of any avian group, and show rates of behavioural innovation and complexity unparalleled in other bird species [106].

214 Observations of thanatological behaviours have been made in several corvid species.
215 Several reports describe a “ceremonial gathering”: an assembly of living individuals near a
216 deceased conspecific. The participants utter alarm calls but seldom touch the corpse or show
217 aggression, in comparison to their predator mobbing or scavenging the corpse of another
218 species [107-111]. Also, compared to the amount of time spent by cetaceans, elephants and
219 primates near corpses (see below), these gatherings tend to be relatively short-lived. There
220 are two reports of objects (feathers, sticks/grass) being placed near the corpse [108-109].
221 Survivors subsequently tend to avoid the place where a dead conspecific is found [112], so
222 much so that effigies have been found useful for pest control [113-114].

223 In many bird species, a dead conspecific generates cautious inspection and/or
224 mobbing behaviours (reviewed in [115]). Lorenz [116] reported his tame jackdaws (*Corvus*
225 *monedula*) attacking him when he carried his black swimming shorts on his hand, and
226 suggested that the likeness of the trunks to a dead jackdaw triggered this mobbing behaviour.
227 Barash [117] paired a predator model – a great horned owl (*Bubo virginianus*) – with either a
228 black cloth or a crow model and obtained similar results: live crows (*Corvus brachyrhynchos*)
229 mobbed these significantly more than the owl model alone. Feathers resembling those of a
230 conspecific may also trigger alarm responses in several crow species [118-120].

231 The primary mode of recognition, therefore, is likely visual: corpses not exhibiting
232 visual cues such as coloured feathers will not elicit responses from live conspecifics. For
233 instance, Heinrich [107] described how a dead crow he attempted to feed to live ravens
234 (*Corvus corax*) was promptly rejected; it was only accepted as food after removal of the
235 feathers, head, wings and feet. Similarly, Lorenz [116] found that adult jackdaws did not mob
236 him if he was holding a young jackdaw before it acquired black feathers, but they did after
237 those feathers grew. In what has been termed the information-gathering hypothesis [7],
238 assemblages around a dead conspecific might serve to acquire information surrounding the
239 death and to assess a potentially dangerous situation. Additionally, assembling corvids might
240 be appraising new social changes in the group [108, 110, 112, 115, 121]. Three experiments
241 formally tested these hypotheses [112, 121, 122]. In scrub-jays (*Aphelocoma californica*),
242 corpses of conspecifics and similar-sized heterospecifics elicit aggregations and site
243 avoidance [122]. A corpse in prone posture elicits cacophonous aggregations, whereas an

upright one elicits mobbing behaviour [121], see also Swift & Marzluff, this issue). Moreover, unlike dead conspecifics, corpses of pigeons (*Columba livia*) elicit little reaction in crows. Interestingly, pigeons are similarly low-responsive to dead pigeons, suggesting that this species processes and evaluates the situation differently from crows [112]. Earlier research on wood pigeons (*Columba palumbus*) used models and, showed that pigeons tend to avoid corpses of conspecifics as a default response [123-124], which contrasts with corvids' initial curiosity.

Studies on crows have not yet explored how the social relationship with the dead affects the interactions of the living, particularly in the case of pair-bonding corvids, although this has been alluded to in single-case reports [108, 111] (see also Section 5). In addition, compared to the taxa discussed next, corvids show limited prosocial tendencies [125], including little regard for conspecifics beyond kin or mate; this may explain their shorter-duration and more frequently agonistic responses to corpses compared to non-human primates, proboscids and cetaceans.

Non-human primates. Currently, more is known about thanatological behaviours in non-human primates than any other vertebrate taxon, and include mobbing/alarm calling, aggression, dead infant carrying, vigils and visitations of the corpse. Physical interactions with the corpse include grooming, gentle touching, poking, attempted sexual mounting, dragging, rough touching, hair-plucking, beating, and even cannibalism (reviewed in [105]; see also Anderson, this issue, Watson & Matsuzawa, this issue).

Dead infant carrying is a prevalent behaviour throughout Old and New World anthropoid primates, and can last from a few hours to a few months. Reports of extended carrying behaviour exist for great apes [126-129] and Old World monkeys [130-133], with the largest study, on Japanese macaques, documenting 157 cases over a 24-year period [134]. Several hypotheses have been proposed to explain such behaviour, not necessarily mutually exclusive: infants live or dead are perceptually attractive to females, maternal hormones involved in mother-infant bonding likely reinforce carrying behaviour, and some behaviours (such as removal of larvae by grooming) and climatic factors (such as high altitude or low humidity) can contribute to preserving the corpse for extended carrying (reviewed in [105]).

Contrary to the mother, other adult group members show little interest in the dead infant, engaging much more with live ones [131, 135-138], although periodic inspections and attempts to play with and carry a mummified corpse (e.g., [139]) have been reported. Instances of guarding the infant corpse or its mother against approaches by other group members have also been witnessed [138, 140-143].

To what extent primates' (or indeed any taxon's) responses to the dead are shaped by learning is an intriguing question. Witnessing death events can allow information-gathering about various sets of cues associated with the phenomenon that can be retrieved on similar subsequent encounters; active information seeking in such situations has been suggested, for example, in chimpanzees [144]. With respect to the extended carrying of dead infants, the eventual abandonment of the corpse by a mother may reflect her acquisition of some component of death-awareness, through a combination of visual, olfactory and behavioural cues – or their lack of correspondence with those emitted by live infants. Social learning may also shape some thanatological responses: it has been suggested that witnessing dead-infant carrying may promote the behaviour in mothers experiencing their own infant's death [139].

Experimental studies of thanatological responses in wild primates are largely lacking in comparison with corvids. Allen and Hauser [145] proposed an experiment using playback calls (as done with vervet monkeys (*Chlorocebus aethiops*)) with recently dead infants, to study concept attribution (e.g., cognizance of death) in non-human primates. Females, they argued, when presented with the playback would (1) orient towards the speaker and act as if the infant were alive, (2) respond in a distressed manner and search for the infant, or (3) not react at all and continue engaging in ongoing activities. To our knowledge this experiment has never been implemented, possibly due to ethical concerns. However, a variation was conducted in a study of the strength of male-female relationships in free-ranging chacma baboons (*Papio ursinus*) [146]. The authors found that males responded to a female's call if there had been a close association ('friendship') between them, but not if the female's infant had recently died. Their interpretation was that females, primarily responsible for maintaining these close associations, ended friendships with males upon their infant's death, either because they no longer needed a male to protect their infants or because they themselves no longer benefited from protection by the male. However, an alternative interpretation is that the

males themselves chose not to respond on the basis of knowing that the infant had died (including, perhaps, knowledge of the event's irreversibility). We further discuss potential experimental approaches for studying death-related psychological states in non-humans in the final section.

Proboscids. The order Proboscidea comprises three extant species, the Asian elephant and the African bush and forest elephants. Wild elephants live in complex fission-fusion societies with female matrilineal kin forming a family unit with close, lifetime bonds. The encephalization quotient of elephants rivals that of primates, and they possess as many cortical neurons as humans do albeit less densely packed than in primate brains (reviewed in [96, 147]).

Like non-human primates, elephants have been observed to surround a dead conspecific, interact directly with it, touch it with their feet or trunks, at times attempt to lift it with either foot or tusks, and vocalizing in apparent distress. They may also guard the body against predators or other conspecifics and revisit the corpse in the following days [148-151]. Adult females have also been observed carrying dead infants weeks after death [152-154].

Unlike non-human primates observed to date (but see [155]), elephants occasionally cover dead conspecifics with branches, leaves or soil, and may attempt to patch wounds on the dead with dirt or put food in their mouth [21, 22, 148, 153, 156]. It is important to consider these behaviours in the context of the elephant's social repertoire with live conspecifics and heterospecifics. Elephants have reportedly buried humans or other dead animals [157, 205].

Contact behaviours with the corpse include using the trunk to inspect the head and body; even the torso may be used for such inspections. Pulling and stepping over the corpse has been observed, as have scent-related behaviours such as sniffing the corpse with tip of the trunk and displaying the flehmen response (touching the tip of the trunk to the openings of the vomeronasal organ). Elephants may also put the trunk in their mouths to assess gustatory information about the corpse [151, 158]. Elephants show striking responses to the bones of other elephants, particularly skulls and tusks, carefully inspecting them [21, 22, 159]. McComb et al. [160] showed experimentally that African elephants are primarily attracted to tusks in comparison to skulls, pay more attention to conspecific skulls than other objects, and

show no evidence of recognizing skulls of familiar conspecifics. The attraction to tusks might be because they represent an externally visible cue to identity that is consistent across life and death.

Playback of calls of dead elephants to live group members has also been attempted [161]. When vocalizations of a female were broadcast to her family unit 3 and 23 months after she had died, group members responded with contact calls each time, even approaching the speaker (but did not do so in control trials involving the vocalisations of unfamiliar individuals), suggesting long-term memory and recognition. As it was not specified whether the group members had directly observed the death or seen the female's corpse, it is unknown whether responses to playback calls would differ depending on such knowledge.

Cetaceans. Thanatological behaviour among cetaceans (whales, dolphins and porpoises) is also becoming increasingly well documented and shows many parallels with primate and proboscidean data. The vast majority of reports (compiled in Reggente et al., this issue; see also [27] for a recent review) concern interactions with dead calves or juveniles; carrying their carcasses has been documented in various dolphin and whale species. Indeed, the behaviour has been observed worldwide and in a range of environments including open oceans bays and inlets, and rivers [162]. Although carrying can be for extended periods, due to the nature of the aquatic environment rapid decomposition limits carrying duration in comparison to, for example, primates in dry habitats. Carrying typically involves holding the calf on the dorsal fin, against the melon or in the mouth. Along with transport, potentially breathing-related behaviours such as lifting the corpse to the surface of the water and pushing it down have been observed (e.g. [163-164]).

Aside from transport, several other categories of behaviours have been documented, including striking the corpse, non-contact attendance such as stationing next to the corpse, and sexual arousal and copulation (towards adults only; e.g., [165]). Unrelated individuals also occasionally interact with corpses, and carriers of an infant corpse are frequently seen surrounded by other pod members swimming in cohesive, possibly protective formations [162].

Like proboscids, cetaceans possess a keen sense of hearing that likely plays an important role in navigating their physical and social environments [166]; however, most cetaceans do not possess a sense of smell or taste [167]. This is likely to impact both the sensory drivers and the nature of their interactions with the dead. Visual cues (presence of wounds, lack of autonomous movement) and lack of auditory cues (vocalisations) are the most likely sources of information about a deceased conspecific's state.

Vertebrate Species in Context. Outside of the taxa discussed above, various mammalian species including giraffes [168-171], otters [172], dingoes [173], seals and sea lions [111, 174-176] and manatees [177] have been observed stationing around, manipulating, or carrying their dead infants for extended periods of time. Phylogenetically ancient maternal caretaking mechanisms continue to operate even after the offspring has died in both mammalian and avian taxa. On a proximate level, the mother may perceive the infant's condition as ambiguous, or she may anticipate that the infant will yet recover, whereupon she continues her caregiving. On an ultimate level, her actions likely represent behavioural error because of the cost of too readily abandoning a potentially temporarily unresponsive infant. A transitional phase ensues which can vary widely (days, weeks or months), during which the mother will carry or stay in close proximity and interact with the corpse (e.g. inspecting, grooming, licking); this phase will decrease over time, culminating in abandonment or occasional consumption of the corpse (see below).

Nonetheless, corvids, primates, proboscids and cetaceans appear to exhibit the greatest similarities in thanatological behaviours. This is surprising as they do not share a recent evolutionary past and occupy different ecological niches. What they do have in common, however, are complex societies, extended parental care and large brains. Hence, the parallels among these taxa in thanatological responses may be the result of similar perceptual-cognitive processing rules that evolved in the context of increasingly complex social environments. Responses to adult conspecific corpses are both stronger and longer than in other taxa, in which the most common response is avoidance (e.g., rodents [87]). Alternatively, the fewer occurrences of thanatological behaviours reported in other vertebrate species could be due to observation bias (see Section 5 for further discussion).

4. THE “UNCANNY” CORPSE

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

4.1 Threat Assessment Mechanisms

Brains coupled to nervous systems evolved as a means to process ecologically relevant information, and to orchestrate adaptive interactions with the surrounding world. They emerged to deal with the challenges that arise from the physical and social environments, and as these became increasingly complex, so did organisms and their brains [40, 178-179]. Detecting cues to the presence of life-threatening risks remains critical for animals, and natural selection has equipped organisms with and without large brains to do this. However, with associative learning, animals no longer adapted only through evolutionary time, but also within their lifetimes via experience-based behavioural adjustments. Thus, cognition and memory, capacities shaped by natural selection, are critical in regulating expectation, detecting discrepancies and anticipating events.

The corpse, a highly salient object, represents a conceptual novelty (any familiar object displayed in unfamiliar configurations or unfamiliar settings) (*sensu* [180]). Comparative neuroimaging research has revealed that novel stimuli are encoded by the hippocampus [181] and the amygdala [182], and damage to these areas diminishes fear and vigilance to threat (reviewed in [183]).

Cross et al. [187] used PET scans to examine cerebral circuitry involved in integrating visual cues into behavioural responses in crows. Crows possess brain regions analogous to the hippocampus and amygdala in mammals that are activated during potentially dangerous situations. The sight of a novel person holding a dead crow activated visual pathways, and

the hippocampus while the amygdala was significantly activated by a predator stimulus (a hawk). These patterns of activity were explained as distinct processing activities when gathering novel threat information (person holding a dead crow) versus retrieving past fear information (mounted hawk).

4.2 The Uncanny Valley

Corpses, as passive entities, defy expectations, provoke emotions and generate various behaviours in the living. Notably, they present a conflicting mixture of presence (odour, wounds, vermin) and absence of cues (movement, sound, body heat).. This contradiction is illustrated by the dual approach/avoidance and exploratory/fearful reactions when encountering a dead body. Paying attention towards dead conspecifics is, as previously discussed, evolutionarily relevant, since the corpse might provide information about potential predation events or a pathogen hazard. Furthermore, taking a proximate approach, the living may be responding to novelty in the form of something “uncanny”.

The uncanny valley phenomenon was originally proposed by roboticist Masahiro Mori [184, 188] to describe the eerie feeling humans experience upon encountering a human replica, and we suggest that it also applies to thanatological responses in non-human animals. Mori used examples such as hand replicas and dead bodies to describe the drop in emotional valence the closer something resembles living specimens of our own species, movement being a key factor in the intensification of eeriness. Cognitive hypotheses posit that an uncanny eliciting stimulus remains in a category boundary or provokes a perceptual mismatch, two explanations that are not necessarily mutually exclusive [189] and not necessarily related to cadavers. An interesting example of this is Goodall’s description of chimpanzees’ fearful and aggressive responses towards physically deformed conspecifics affected by poliomyelitis who moved in unusual ways [190]. At the ultimate level, an adaptive pathogen-avoidance mechanism could be at play, whereby abruptly acquired physical abnormalities in conspecifics trigger a disgust response in other group members (sensu [191-192]).

Steckenfinger and Ghazanfar [193] attempted to test the uncanny valley effect in rhesus macaques and found that both humans and macaques display the same aversion to

realistic reconstructions of conspecific faces, particularly, as predicted by Mori, if these were moving (also see [139] for an example of aversion to a “moving” – i.e. dragged – corpse among wild chimpanzees). This suggests that the mechanism causing uncanny-valley-like responses was present already in the common ancestor of Old World monkeys and *Homo sapiens*. Experimental work with human infants suggests that the uncanny valley phenomenon emerges in the first year of life, likely due to perceptual narrowing and learning/differentiation processes [194]. Regarding the quality of dynamic cues, research suggests that the more natural movement is (see biological motion) the more likely it is to be accepted by human subjects (suggesting less of an uncanny effect) [185]. Some types of stimuli such as androids or corpses likely fail sensory/cognitive scrutiny based on these learning processes, thus triggering an aversive response.

4.3 Animacy Detection Malfunction

In non-human primates, life detection is part of a series of Core Knowledge Systems [195], in this case, the Core System of Agency. The Core Knowledge Theory proposes that hard-wired cognitive skills shape mental representations about the world. It remains unclear how many subsystems contribute to agency representation and how they are inter-related; however, some have been unveiled by developmental and comparative cognitive scientists [195-197]. The Animate/Inanimate Distinction level likely operates through dual Core Knowledge Systems specialized for dealing with animate and inanimate entities: the aforementioned Core System of Agency (C.S.A.) and the Core System of Object (C.S.O.), respectively. Contrary to agents, objects are predictable. They are inert, moving only when external force is applied to them, and as such they exhibit no contingency or any of the other traits associated with agency: they neither act nor react, but are acted upon by the living agents.

We suggest Animacy Detection Malfunction as a cognitive term for the conflicting responses exhibited by vertebrate taxa upon encountering dead conspecifics. The agency system is not perfect but prone to error; however in terms of its primary purpose (agent detection), it normally functions well. Inspired by earlier views [188, 198, 199] animacy detection malfunction is defined as the conflicting cognitive process upon seeing a corpse brought about by perceptual mismatch ultimately causing a violation of expectation. The

mismatch stems from the absence of dynamic cues to animacy with the presence of static cues to animacy and is intensified by individual recognition of the dead conspecific. The corpse then has both animate and inanimate attributes triggering a conflict between the Core Knowledge System of Agency and the Core Knowledge System of Object.

4.4 Death Detection Mechanism

Humans have long dealt with conflicting stimuli from corpses through cultural mortuary practices which are rooted in the deep hominid past [200]. Barrett & Behne [201] argued for the existence of a death detection mechanism, evolved through the course of human evolution, contending that reliable visual cues indicating death, such as fatal disruptions of the body envelope (e.g., decapitation, severe mutilation), were important in the recategorisation from “living” to “dead” in humans. This can be illustrated with reference to predator detection accuracy, where failure results in death. The ability to discriminate a live predator (snake, leopard, crocodile) from a dead one allows for the activation of different behavioural decision-making outcomes with implications for survival [201].

In a study of grief after the loss of a companion animal, White et al. [202] found that humans viewing a corpse that exhibited reliable cues for death (i.e. grievous injuries, disruption of the body envelope) displayed less vigilant behaviour than when the corpse was intact. What they termed “false recognitions” (incorrect attributions of sight and sound to the deceased) were also more frequent when the corpse was intact. Adopting and expanding on Barrett and Behne’s [201] death detection mechanism, these authors suggest that natural selection shaped the increase in vigilance behaviour whenever a valuable partner was missing, and that attending to reliable cues of death was selected for throughout human evolutionary history.

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

curated hide of a juvenile chimpanzee, and the corpse of an infant chimpanzee. Some of the objects elicited intense fear or panic (in decreasing order: movable chimpanzee skull, snake cast, movable spider monkey skin, chimpanzee death mask), which Hebb interpreted as fears due to conflict; he suggested that the sight of mutilated bodies aroused an incompatibility at both the perceptual and at the cognitive level [198].

Butler [203] tested rhesus macaques in test-box where they could see through an opening into another box..This other box contained live snakes, a live conspecific, an anesthetized conspecific or a dead conspecific with its head on its outstretched hands. Butler predicted that the more frightful the stimulus, the more suppressed the viewing behaviour would be. However, this was not the case, and Butler explained the monkeys' reactions as a possible result of a psychological barrier between the subjects and the objects since no physical contact was possible. The decapitated monkey did elicit more looks than the live one, even though mean looking times were higher for the latter. This result might reflect a configural incongruity in the corpse eliciting a greater number of viewings but decreased overall looking time due to aversion (sensu the uncanny valley phenomenon).

How do these considerations help us advance our understanding of death awareness in non-humans in their natural environment? Boesch [155] has suggested that wild chimpanzees have a capacity for the 'causation' subcomponent of a full-blown awareness of death. Chimpanzees of the Taï Forest (Ivory Coast) face higher predation risks than many other chimpanzee communities [142]; they exhibit more fearful responses to individuals that died of disease (10 cases) than those that show wounds due to leopard predation (5 cases). Furthermore, Taï chimpanzees lick the wounds of injured group members, but not the dead. If the reason for these differences lies in an understanding of reliable cues for death (grievous wounds, severe disruptions of the body envelope), then chimpanzees may have an implicit awareness of death, not only distinguishing between dead and alive, but also between different manners of death, potentially providing evidence for the subcomponent of causation.

5. CONCLUSIONS AND FUTURE WORK

Our review has brought together observations of living individuals' responses to dead conspecifics in invertebrates and vertebrates, evidence regarding the sensory bases of detecting life and death in others, and potential cognitive underpinnings for animals' awareness of death. We suggest that phylogenetically ancient responses relating to death that are present in many animals exist not only for specific predator detection but also form part of a generalized threat detection mechanism. Presumably in corvids, cetaceans, proboscids and non-human primates, these mechanisms run in parallel with living-dead discrimination processes based on associative concepts. We also argue that analogical reasoning is a sine qua non condition for human-like death awareness with all of its main subcomponents (Universality, Irreversibility, Cessation and Causation).

Many authors have called for more and better data on animals' responses to the dead (including a number of contributors to the present issue - e.g., Watson & Matsuzawa; Reggente et al.; Anderson) to advance comparative thanatology - greater taxonomic breadth, more quantitative descriptions and more systematic phylogenetic comparisons. While fully supporting these calls, we also advocate controlled experiments to probe the sensory and cognitive bases of the detection of death and its associated psychological states. For example, presenting taxidermy specimens of dead individuals of various species and in various poses might elucidate what cues trigger responses to the dead, and what adaptive explanations might lie behind animals' interest in the dead [112, 121, 122]. In addition, further manipulation of stimuli – such as the computer-generated images used by Steckenfinger and Ghazanfar [193] to probe the uncanny valley effect in monkeys – could permit analysis of underlying cognition. What cognitive processes are tapped into when detecting life and death in others? How are cues that conflict within or between modalities (e.g., a decapitated but moving individual, or a moving individual smelling of necromones) resolved in different taxa, and can cross-species comparisons of cue hierarchy inform our reconstruction of phylogenetically ancient vs derived mechanisms for death detection? How do parameters such as state of decomposition, visible cues indicating cause of death, social/kin relationship of corpse and observer, previous experiences with death, etc. influence responses in different taxa? Of course, such experiments need careful ethical consideration, to minimise distress to subjects.

In addition, playback experiments like those proposed by Allen and Hauser [145] could probe how living individuals conceptualise dead conspecifics, stress assessment (such as analysis of glucocorticoid levels, [204]) can reveal physiological reactions to the loss of conspecifics with close or distant social or kin bonds, and non-invasive neuroimaging studies, [187] might demonstrate how animals process corpses on the animate-inanimate spectrum. While both technically and ethically challenging, such a research programme may go a long way towards elucidating the proximate and ultimate drivers of thanatological responses across taxa.

Authors' Contributions

The authors conceived and wrote the manuscript together.

Competing Interests

We have no competing interests.

References

1. Darwin C. 1871 *The descent of man*. London: John Murray.
2. Griffin DR. 1976 *The question of animal awareness*. Rockefeller University Press.
3. Heidegger M. 1971 *The thing: poetry, language, thought*. New York: Harper and Row.
4. Solomon S, Greenberg J, Pyszczyński T. 2015 *The worm at the core*. Penguin Random House.
5. Becker E. 1973 *The denial of death*. New York: Free Press.
6. Dobzhansky T. 1967 *The Biology of the Ultimate Concern*. New York: New American Library.
7. Anderson JR. 2016 Comparative thanatology. *Curr. Biol.* **26**, R553-R556. (<https://doi.org/10.1016/j.cub.2015.11.010>).
8. Rackham H, (Translator) Pliny, The Elder (Author). 1938 *Pliny's natural history*.

- 602 Heinemann: Loeb Classical Library.
- 603 9. McNamee G. (translator), Aelianus C. (Author). 2011 *Aelian's on the nature of animals*.
604 Trinity University Press.
- 605 10. Forbes J. 1813 *Oriental memoirs*. London: White, Cochrane.
- 606 11. Brown AE. 1879 Grief in the chimpanzee. *Am. Nat.* **13**,173-175.
- 607 12. Maxwell WH. 1832 *The field book or sports and pastimes of the british islands*. London:
608 W. Tweedie Strand.
- 609 13. Reischek A. 1886 Notes on the habits of some New Zealand birds. *Trans. Proc. New*
610 *Zeal. Inst.* **18**, 96-107.
- 611 14. Van der Kemp J. 1806 Account of a journey to the Booshuanas of Southern Africa. In:
612 *Barrow's Cochinchina*. London: Cadell & Davies.
- 613 15. Marryat RN. 1887 *The mission or scenes in Africa*. London: George Routledge and
614 Sons.
- 615 16. Sherrin RAA, Wallace JH, Leys TW. 1890 *Early history of New Zealand*. Auckland: H
616 Brett.
- 617 17. Murray JH. 1871 *Travels in Uruguay*. London: Longmans & Co.
- 618 18. Coomstock JL. 1829 *Natural history of quadrupeds with engravings on a new plan*
619 *exhibiting their comparative size adapted to the capacities of youth with authentic*
620 *anecdotes illustrating the habits and characters of the animals together with reflections,*
621 *moral and religious*. Hartford: DF. Robinson & Co.
- 622 19. Brown T. 1835 *Anecdotes of the animal kingdom containing illustrations of the*
623 *characters, habits, dispositions and capabilities of quadrupeds, birds, fishes, reptiles*
624 *and insects*. Glasgow: Archibald Fullarton & Co.
- 625 20. Steller GW, Miller W, (Translator), Miller JE (Translator), Royster P (Transcriber and
626 editor),1751 *De bestiis marinis, or, the beasts of the sea (1751)*. Faculty Publications,
627 UNL Libraries. **17**.
- 628 21. Douglas-Hamilton I, Douglas-Hamilton O. 1975 *Among the elephants*. London: Collins
629 & Harvill Press.
- 630 22. Moss C. 1992 *Echo of the elephants: the story of an elephant family*. London: William
631 Morrow.

- 632 23. Anderson JR. 2011 A primatological perspective on death. *Am. J. Primatol.* **73**, 410-
633 414. (<https://doi.org/10.1002/ajp.20922>).
- 634 24. López-Riquelme GO, Fanjul-Moles ML. 2013 The funeral ways of social insects: Social
635 strategies for corpse disposal. *Trends Entomol.* **9**, 71-129.
- 636 25. Sun Q, Zhou X. 2013. Corpse management in social insects. *Int. J. Biol. Sci.* **9**, 313.
637 (<https://doi.org/10.7150/ijbs.5781>).
- 638 26. Piel AK, Stewart FA. 2015 Non-human animal responses towards the dead and death:
639 a comparative approach to understanding the evolution of human mortuary practices.
640 In: *Death Rituals and Social Order in the Ancient World: Death Shall Have No*
641 *Dominion*. Renfrew, C.; Boyd, M. J.; Morley, I. (Eds). Cambridge University Press.
642 (<https://doi.org/10.1017/CBO9781316014509.003>).
- 643 27. Bearzi G, Eddy L, Piwetz S, Reggente MAL, Cozzi B. 2017 Cetacean behavior toward
644 the dead and dying. In: *Encyclopedia of Animal Cognition and Behavior*. Vonk J,
645 Shackelford TK. (Eds.). Springer International Publishing.
- 646 28. Thurman SM, Lu H. 2013 Complex interactions between spatial, orientation, and
647 motion cues for biological motion perception across visual space. *J. Vision.* **13**, 1-18.
648 (<https://doi.org/10.116/13.2.8>).
- 649 29. Wolpert L. 2003 Causal belief and the origins of technology. *Phil. Trans. R. Soc. Lond.*
650 *A.* **361**, 1709-1719. (<https://doi.org/10.1098/rsta.2003.1231>).
- 651 30. Davidov Y, Jurkevitch E. 2009 Predation between prokaryotes and the origin of
652 eukaryotes. *BioEssays.* **31**, 748-757. (<https://doi.org/10.1002/bies.200900018>)
- 653 31. Knoll AH. 2015 *Life on a young planet: the first three billion years of evolution on earth*.
654 New Jersey: Princeton University Press.
- 655 32. Erwin DH, Laflamme M, Tweedt SM, Sperling EA,, Pisani D, Peterson KJ. 2011 The
656 Cambrian conundrum: early divergence and later ecological success in the early
657 history of animals. *Science.* **334**, 1091-1097.
658 (<https://doi.org/10.1126/science.1206375>).
- 659 33. Gingras M, Hagadorn JW, Seilacher A, Lalonde SV, Pecoits E, Petrash D, Konhauser
660 KO. 2011 Possible evolution of mobile animals in association with microbial mats.
661 *Nat. Geosci.* **4**, 372-375. (<https://doi.org/10.1038/ngeo1142>).

- 662 34. Holland PW. 2015 Did homeobox gene duplications contribute to the Cambrian
663 explosion? *Zool. Lett.* 1, 1-8. (<https://doi.org/10.1186/s40851-014-0004-x>)
- 664 35. Northcutt RG. 2012 Evolution of centralized nervous systems: two schools of
665 evolutionary thought. *Proc. Nat. Acad. Sci.* **109**, 10626-10633.
666 (<https://doi.org/10.1073/pnas.1201889109>)
- 667 36. Parker A. 2003 *In the blink of an eye: how vision kick-started the big bang of evolution*.
668 New York: Basic books.
- 669 37. Graziano MSA. 2014 Speculations on the evolution of awareness. *J. Cognitive*
670 *Neurosci.* 26, 1300-1304. (https://doi.org/10.1162/jocn_a_00623).
- 671 38. Ginsburg S, Jablonka E. 2010 The evolution of associative learning: A factor in the
672 Cambrian explosion. *J. Theor. Biol.* **266**, 11-20.
673 (<https://doi.org/10.1016/j.jtbi.2010.06.017>).
- 674 39. Trestman M. 2013 The Cambrian explosion and the origins of embodied cognition. *Biol.*
675 *Theory.* **8**, 80-92. (<https://doi.org/10.1007/s13752-013-0102-6>).
- 676 40. Feinberg TE, Mallatt J. 2013 The evolutionary and genetic origins of consciousness in
677 the Cambrian Period over 500 million years ago. *Front. Psychol.* **4**, 1-27.
678 (<https://doi.org/10.3389/fpsyg.2013.00667>).
- 679 41. Johnson MH. 2006 Biological motion: a perceptual life detector? *Curr. Biol.* **16**, R376-
680 R377. (<https://doi.org/10.1016/j.cub.2006.04.008>).
- 681 42. Troje NF, Westhoff C. 2006 The inversion effect in biological motion perception:
682 Evidence for a "life detector"? *Curr. Biol.* **16**, 821-824.
683 (<https://doi.org/10.1016/j.cub.2006.03.022>).
- 684 43. Vallortigara G, Regolin L. 2006 Gravity bias in the interpretation of biological motion by
685 inexperienced chicks. *Curr. Biol.* **16**, R279-R280.
686 (<https://doi.org/10.1016/j.cub.2006.03.052>).
- 687 44. Mascalzoni E, Regolin L, Vallortigara G. 2010 Innate sensitivity for self-propelled
688 causal agency in newly hatched chicks. *P. Natl. Acad. Sci. USA.* **107**, 4483-4485.
689 (<https://doi.org/10.1073/pnas.0908792107>).
- 690 45. Simion F, Regolin L, Bulf H. 2008 A predisposition for biological motion in the newborn
691 baby. *P. Natl. Acad. Sci.* **105**, 809-813. (<https://doi.org/10.1073/pnas.0908792107>).

- 692 46. Bardi L, Regolin L, Simion F. 2011 Biological motion preference in humans at birth: role
693 of dynamic and configural properties. *Dev. Sci.* **14**, 353–359.
694 (<https://doi.org/10.1111/j.1467-7687.2010.00985.x>).
- 695 47. Nakayasu T, Watanabe E. 2014 Biological motion stimuli are attractive to medaka fish.
696 *Anim. Cogn.* **17**,559-575. (<https://doi.org/10.1007/s10071-013-0687-y>).
- 697 48. Troje NF, Aust U. 2013 What do you mean with “direction”? Local and global cues to
698 biological motion perception in pigeons. *Vision Res.* **79**, 47-55.
699 (<https://doi.org/10.1016/j.visres.2013.01.002>).
- 700 49. MacKinnon LM, Troje NF, Dringenberg HC. 2010 Do rats (*Rattus norvegicus*) perceive
701 biological motion?. *Exp. Brain Res.* **205**, 571-576. ([https://doi.org/10.1007/s00221-010-](https://doi.org/10.1007/s00221-010-2378-0)
702 [2378-0](https://doi.org/10.1007/s00221-010-2378-0)).
- 703 50. Blake R. 1993 Cats perceive biological motion. *Psychol. Sci.* **4**, 54-57.
- 704 51. Herman LM, Morrel-Samuels P, Pack AA. 1990 Bottlenosed dolphin and human
705 recognition of veridical and degraded video displays of an artificial gestural language.
706 *J. Exp. Psychol.* **119**,215.
- 707 52. Brown J, Kaplan G, Rogers LJ, Vallortigara G. 2010 Perception of biological motion in
708 common marmosets (*Callithrix jacchus*): by females only. *Anim. Cogn.* **13**, 555-564.
709 (<https://doi.org/10.1007/s10071-009-0306-0>).
- 710 53. Oram MW, Perrett DI. 1996 Integration of form and motion in the anterior superior
711 temporal polysensory area (STPa) of the macaque monkey. *J. Neurophysiol.* **76**, 109-
712 129. (<https://doi.org/10.1152/jn.1996.76.1.109>).
- 713 54. Parron C, Deruelle C, Fagot J. 2007 Processing of biological motion point-light displays
714 by baboons (*Papio papio*). *J. Exp. Psych. Anim. Behav. Proc.* **33**,381-391.
715 (<http://dx.doi.org/10.1037/0097-7403.33.4.381>).
- 716 55. Tomonaga M. 2001 Visual search for biological motion patterns in chimpanzees (*Pan*
717 *troglodytes*). *Psychologia.* **44**,46-59.
- 718 56. Johnson MH. 2005 Subcortical face processing. *Nat. Rev. Neurosci.* **6**,766-774.
719 (<http://doi:10.1038/nrn1766>).
- 720 57. Parr LA. 2011 The evolution of face processing in primates. *Philos. T. Roy. Soc. B.*
721 **366**, 1764-1777. (<https://doi.org/10.1098/rstb.2010.0358>).

- 722 58. Sugita Y. 2008 Face perception in monkeys reared with no exposure to faces. *Proc.*
723 *Natl. Acad. Sci. USA.* **105**,394-398. (<https://doi.org/10.1073/pnas.0706079105>).
- 724 59. Shimizu Y, Johnson SC. 2004 Infants' attribution of a goal to a morphologically
725 unfamiliar agent. *Developmental Science.* **7**, 425-430. ([https://doi.org/10.1111/j.1467-](https://doi.org/10.1111/j.1467-7687.2004.00362.x)
726 [7687.2004.00362.x](https://doi.org/10.1111/j.1467-7687.2004.00362.x)).
- 727 60. Csibra G. 2008 Goal attribution to inanimate agents by 6.5-month-old infants.
728 *Cognition.* **107**, 705-717. (<https://doi.org/10.1016/j.cognition.2007.08.001>).
- 729 61. Opfer JE, Gelman SA. 2010 Development of the animate-inanimate distinction. In: *The*
730 *Wiley-Blackwell Handbook of Childhood Cognitive Development.* Goshwami U. (Ed),
731 pp. 213-238. New York: Wiley-Blackwell.
- 732 62. Woodward AL. 1998 Infants selectively encode the goal object of an actor's reach.
733 *Cognition.* **69**, 1-34. ([https://doi.org/10.1016/S0010-0277\(98\)00058-4](https://doi.org/10.1016/S0010-0277(98)00058-4)).
- 734 63. Woodward AL. 1999 Infants' ability to distinguish between purposeful and non-
735 purposeful behaviors. *Infant Behav. Dev.* **22**, 145-160. ([https://doi.org/10.1016/S0163-](https://doi.org/10.1016/S0163-6383(99)00007-7)
736 [6383\(99\)00007-7](https://doi.org/10.1016/S0163-6383(99)00007-7)).
- 737 64. Woodward AL, Sommerville JA, Guajardo JJ. 2001 How infants make sense of
738 intentional action. In: *Intentions and intentionality: Foundations of social cognition.*
739 Malle BF, Moses LJ, Baldwin DA (Eds), pp. 149-169. Massachusetts: The MIT Press.
- 740 65. Hofer T. Hauf P. Aschersleben G. 2005 Infant's perception of goal-directed actions
741 performed by a mechanical device. *Infant Behav. Dev.* **28**, 466-480.
742 (<https://doi.org/10.1016/j.infbeh.2005.04.002>).
- 743 66. Daum MM, Gredebäck G. 2011 Spatial cueing by referential human gestures, arrows
744 and mechanical devices. *Int. J. Mind Brain Cognition.* **2**, 113-126.
- 745 67. Phillips W, Barnes JL, Mahajan N, Yamaguchi M, Santos LR. 2009 'Unwilling versus
746 unable': capuchins' (*Cebus apella*) understanding of human intentional
747 action.*Developmental Sci.* **12**, 938-945. ([https://doi.org/10.1111/j.1467-](https://doi.org/10.1111/j.1467-7687.2009.00840.x)
748 [7687.2009.00840.x](https://doi.org/10.1111/j.1467-7687.2009.00840.x)).
- 749 68. Kupferberg A, Glasauer S, Burkart JM. 2013 Do robots have goals? How agent cues
750 influence action understanding in non-human primates. *Behav. Brain Res.* **246**, 47-54.
751 (<https://doi.org/10.1016/j.bbr.2013.01.047>).

- 752 69. Slaughter, V. 2005 Young children's understanding of death. *Aust. Psychol.* **40**, 179-
753 186. (<https://doi.org/10.1080/00050060500243426>).
- 754 70. Caramazza A, Shelton JR. 1998 Domain-specific knowledge systems in the brain: The
755 animate-inanimate distinction. *J. Cognitive Neurosci.* **10**, 1-34.
756 (<https://doi.org/10.1162/089892998563752>).
- 757 71. Naselaris T, Stansbury DE, Gallant JL. 2012 Cortical representation of animate and
758 inanimate objects in complex natural scenes. *J. Physiol-Paris.* **106**,239-249.
759 (<https://doi.org/10.1016/j.jphysparis.2012.02.001>).
- 760 72. Kiani R, Esteky H, Mirpour K, Tanaka K. 2007 Object category structure in response
761 patterns of neuronal population in monkey inferior temporal cortex. *J. Neurophysiol.* **97**,
762 4296-4309. (<https://doi.org/10.1152/jn.00024.2007>).
- 763 73. Kriegeskorte, N, Mur M, Ruff DA, Kiani R, Bodurka J, Esteky H, Tanaka K, Bandettini
764 PA. 2008 Matching categorical object representations in inferior temporal cortex of man
765 and monkey. *Neuron.* **60**,1126-1141. (<https://doi.org/10.1016/j.neuron.2008.10.043>).
- 766 74. Hagedaars MA, Oitzl M, Roelofs K. 2014 Updating freeze: aligning animal and human
767 research. *Neurosci. Biobehav. R.* **47**, 165-176.
768 (<https://doi.org/10.1016/j.neubiorev.2014.07.021>).
- 769 75. Humphreys RK, Ruxton GD. 2018 A review of thanatosis (death feigning) as an anti-
770 predator behaviour. *Behav. Ecol. Sociobiol.* **72**,, 22. ([https://doi.org/10.1007/s00265-](https://doi.org/10.1007/s00265-017-2436-8)
771 [017-2436-8](https://doi.org/10.1007/s00265-017-2436-8)).
- 772 76. McAleer P. Pollick FE. 2008 Understanding intention from minimal displays of human
773 activity. *Behav. Res. Methods.* **40**,830-839. (<https://doi.org/10.3758/BRM.40.3.830>).
- 774 77. Johanson G. 1973 Visual perception of biological motion and a model for its analysis.
775 *Percept Psychophys.* **14**. 201-211. (<https://doi.org/10.3758/BF03212378>)
- 776 78. Wilson EO, Durlach NI, Roth LM. 1958 Chemical releaser of necrophoric behavior in
777 ants. *Psyche.* **65**,108-114. (<https://doi.org/10.1155/1958/69391>).
- 778 79. Haskins CP, Haskins EF. 1974 Notes on necrophoric behavior in the archaic ant
779 *Myrmecia Vindex* (Formicidae: Myrmeciinae). *Psyche.* **81**, 258-267.
780 (<https://doi.org/10.1155/1974/80395>).
- 781 80. Choe DH, Millar JG, Rust MK. 2009 Chemical signals associated with life inhibit

- necrophoresis in Argentine ants. *Proc. Natl. Acad. Sci. U S A.* **106**,8251-8255.
(<https://doi.org/10.1073/pnas.0901270106>).
81. López-Riquelme GO, Malo EA, Cruz- López L, Fanjul-Moles ML. 2006. Antennal
olfactory sensitivity in response to task - related odours of three castes of the ant *Atta*
mexicana (hymenoptera: formicidae). *Physiol. Entomol.* **31**, 353-360.
(<https://doi.org/10.1111/j.1365-3032.2006.00526.x>).
82. Rollo, C.D., Yao, M., Rosenfeld, J., Attridge, S., Sidhu, S., Aksenov, V. 2009 The
ancient chemistry of avoiding risks of predation and disease. *Evol. Biol.* **36**, 267–281.
(<https://doi.org/10.1007/s11692-009-9069-4>).
83. Hussain A, Saraiva LR, Ferrero DM, Ahuja G, Krishna VS, Liberles SD, Korsching SI.
2013 High-affinity olfactory receptor for the death-associated odor cadaverine. *Proc.*
Natl. Acad. Sci. **110**, 19579-19584. (<https://doi.org/10.1073/pnas.1318596110>).
84. Oliveira TA, Koakoski G, da Motta AC, Piato AL, Barreto RE, Volpato GL, Barcellos
LJG. 2014 Death-associated odors induce stress in zebrafish. *Hormon. Behav.* **65**,
340-344. (<https://doi.org/10.1016/j.yhbeh.2014.02.009>).
85. Bals JD, Wagner CM. 2012 Behavioral responses of sea lamprey (*Petromyzon*
marinus) to a putative alarm cue derived from conspecific and heterospecific sources.
Behaviour. **149**, 901-923. (<https://doi.org/10.1163/1568539X-00003009>).
86. Hart NS, Collin SP. 2015 Sharks senses and shark repellents. *Integr. Zool.* **10**, 38-64.
(<https://doi.org/10.1111/1749-4877.12095>).
87. Prounis GS. Shields WM. 2013 Necrophobic behavior in small mammals. *Behav.*
Process. **94**, 41-44. (<https://doi.org/10.1016/j.beproc.2012.12.001>).
88. Peterson RS, Batholomew GA. 1967 The natural history and behavior of the California
sea lion. *Am. Soc. Mammal.* **737**, 47-98.
89. Wisman A. Shrira I. 2015 The smell of death: evidence that putrescine elicits threat
management mechanisms. *Front Psychol.* **6**, 1274.
(<https://doi.org/10.3389/fpsyg.2015.01274>).
90. Pinel JP, Gorzalka BB, Ladak F. 1981 Cadaverine and putrescine initiate the burial of
dead conspecifics by rats. *Physiol. Behav.* **27**.819–824. ([https://doi.org/10.1016/0031-9384\(81\)90048-2](https://doi.org/10.1016/0031-9384(81)90048-2)).

- 812 91. Rolan SH, Sorensen PW, Mattson D, Caprio J. 2003 Polyamines as olfactory stimuli in
813 the goldfish *Carassius auratus*. *J. Exp. Biol.* **206**,1683–1696.
814 (<https://doi.org/10.1242/jeb.00338>).
- 815 92. Ulyshen MD, Shelton TG. 2012 Evidence of cue synergism in termite corpse response
816 behavior. *Naturwissenschaften*. 99 89-93.
- 817 93. Clayton NS, Emery NJ. 2007 The social life of corvids. *Curr. Biol.* **17**, R652-R656.
818 (<https://doi.org/10.1016/j.cub.2007.05.070>).
- 819 94. Bates LA, Poole JH, Byrne RW. 2008 Elephant cognition. *Curr. Biol.* **18**,R544-546.
820 (<https://doi.org/10.1016/j.cub.2008.04.019>).
- 821 95. Marino L, Connor RC, Fordyce RE, Herman LM, Hof PR, Lefebvre L, Lusseau D,
822 McCowan B, Nimchinsky EA, Pack AA, Rendell L, Reidenberg JS, Reiss D, Uhen MD,
823 Van der Gucht E, Whitehead H. 2007 Cetaceans have complex brains for complex
824 cognition. *PLoS Biol.* **5**, e139. 0966- 0972.
825 (<https://doi.org/10.1371/journal.pbio.0050139>).
- 826 96. Byrne RW, Bates L, Moss CJ. 2009 Elephant cognition in primate perspective. *Compar.*
827 *Cogn. Behav. Rev.* **4**, 65-79. (<http://dx.doi.org/10.3819/ccbr.2009.40009>).
- 828 97. Veit L, Nieder A. 2013 Abstract rule neurons in the endbrain support intelligent
829 behaviour in corvid songbirds. *Nature Comm.* **4**, 2878.
830 (<http://doi:10.1038/ncomms3878>).
- 831 98. Kondo N, Izawa E-I, Watanabe S. 2012 Crows cross-modally recognize group
832 members but not non-group members. *Proc. R. Soc. B.* **279**,1937–1942.
833 (<https://doi.org/10.1098/rspb.2011.2419>).
- 834 99. Seyfarth RM, Cheney DL. 2015. 3 The Evolution of Concepts about Agents: Or, What
835 Do Animals Recognize When They Recognize an Individual?. *In: The conceptual mind:*
836 *new directions in the study of concepts.* Margolis E, Laurence S. (Eds) p. 57-76.
837 Cambridge, MIT Press.
- 838 100. Gallup GG. 1970 Chimpanzees: self-recognition. *Science.* **167**, 86-87. (
839 <https://doi.org/10.1126/science.167.3914.86>).
- 840 101. Reiss D, Marino L. 2001 Mirror self-recognition in the bottlenose dolphin: A case of
841 cognitive convergence. *Proc. Nat. Acad. Sci.* **98**, 5937-5942.

842 (<https://doi.org/10.1073/pnas.101086398>).

843 102. Plotnik J M, De Waal FB, Reiss D. 2006 Self-recognition in an Asian elephant. *Proc.*
844 *Nat. Acad. Sci.* **103**, 17053-17057. (<https://doi.org/10.1073/pnas.0608062103>).

845 103. Prior H, Schwarz A, Güntürkün O. 2008 Mirror-induced behavior in the magpie (*Pica*
846 *pica*): evidence of self-recognition. *PLoS Biol.* **6**, e202.
847 (<https://doi.org/10.1371/journal.pbio.0060202>).

848 104. Byrne RW. 2016. *Evolving insight*. Oxford: Oxford University Press.

849 105. Gonçalves A, Carvalho S. Death among primates: A review of non-human primate
850 interactions towards their dead and dying. (Manuscript in preparation).

851 106. Taylor AH. 2014 Corvid cognition. *Wires Cogn. Sci.* **5**, 361-372.
852 (<https://doi.org/10.1002/wcs.1286>).

853 107. Heinrich B. 1999 *Mind of the raven: investigating and adventures with wolf-birds*. New
854 York: Harper-Collins.

855 108. Marzluff J, Angell T. 2012 *Gifts of the crow: how perception, emotion, and thought allow*
856 *smart birds to behave like humans*. New York, NY: Free Press.

857 109. Bekoff M. 2007 *The emotional lives of animals: A leading scientist explores animal joy,*
858 *sorrow, and empathy—and why they matter*. Novato: New World Library.

859 110. Miller WR, Brigham RM. 1988 " Ceremonial" Gathering of Black-Billed Magpies (*Pica*
860 *pica*) after the Sudden Death of a Conspecific. *The Murrelet.* **69**, 78-79.

861 111. Pierotti R, Annett C. 2014 We Probably Thought That Would Be True: Perceiving
862 Complex Emotional States in Nonhumans. *Ethnobiol. Letters.* **5**, 15-21.

863 112. Swift KN, Marzluff JM. 2015 Wild American crows gather around their dead to learn
864 about danger. *Anim. Behav.* **109**, 187-197.
865 (<https://doi.org/10.1016/j.anbehav.2015.08.021>).

866 113. Avery ML, Tillman EA, Humphrey JS. 2008 Effigies for dispersing urban crow roosts.
867 *Proc. Vertebr. Pest Conf.* **23**, 84-87.

868 114. Peterson SA, Colwell MA. 2014 Experimental evidence that scare tactics and effigies
869 reduce corvid occurrence. *Nw. Nat.* **95**, 103-112. (<https://doi.org/10.1898/NWN13-18.1>).

870 115. Curio, E. 1993 Proximate and developmental aspects of antipredator behavior. *Adv.*
871 *Stud. Behav.* **22**, 135-238.

- 872 116. Lorenz K. 1952 *King Solomon's Ring*. London: Methuen & Co., Ltd.
- 873 117. Barash DP. 1976 Mobbing behavior by crows: the effect of the "crow-in-distress" model.
874 *The Condor*. 78, 120-120.
- 875 118. Lorenz K. 1971 *Studies in animal and human behavior*. Methuen & Company Limited.
- 876 119. Verbeek NA. 1972 Comparison of displays of the yellow-billed magpie (*Pica nuttalli*)
877 and other corvids. *J. Ornithol.* **113**, 297-314. (<https://doi.org/10.1007/BF01647510>).
- 878 120. Kilham L. 1982 Common crows and a Florida red-shouldered hawk mobbing feathers
879 on the ground. *Fla. Field. Nat.* **10**,23.
- 880 121. Iglesias TL, McElreath R, Patricelli GL. 2012 Western scrub-jay funerals: cacophonous
881 aggregations in response to dead conspecifics. *Anim. Behav.* **84**, 1103-1111.
882 (<https://doi.org/10.1016/j.anbehav.2012.08.007>).
- 883 122. Iglesias, TL, Stetkevich RC, Patricelli GL. 2014 Dead heterospecifics as cues of risk in
884 the environment: Does size affect response? *Behaviour.* **151**, 1-22.
885 (<https://doi.org/10.1163/1568539X-00003120>)
- 886 123. Inglis IR, Isaacson AJ. 1984 The responses of Woodpigeons (*Columba palumbus*) to
887 pigeon decoys in various postures: a quest for a super-normal alarm stimulus.
888 *Behaviour.* **90**, 224-240. (<https://doi.org/10.1163/156853984X00155>).
- 889 124. Inglis IR, Isaacson AJ. 1987 Development of a simple scaring device for woodpigeons
890 (*Columba palumbus*). *Crop Prot.* **6**, 104-108. ([https://doi.org/10.1016/0261-](https://doi.org/10.1016/0261-2194(87)90107-4)
891 [2194\(87\)90107-4](https://doi.org/10.1016/0261-2194(87)90107-4)).
- 892 125. Lambert ML, Massen JJM, Seed AM, Bugnyar T, Slocombe KE. 2017 An 'unkindness'
893 of ravens? Measuring prosocial preferences in *Corvus corax*. *Anim. Behav.* **123**, 383-
894 393. (<https://doi.org/10.1016/j.anbehav.2016.11.018>).
- 895 126. Nishida T. 1973 *The Children of the Mountain Spirits: Search for the Social Structure of*
896 *Chimpanzees*. Tokyo: Chikuma-shobo. (In Japanese).
- 897 127. Hosaka K, Matsumoto-Oda A, Huffman MA, Kawanaka K. 2000 Reactions to Dead
898 Bodies of Conspecifics by Wild Chimpanzees in the Mahale Mountains, Tanzania .
899 *Primate Res.* **16**, 1-15. (Japanese with English Summary).
900 (<https://doi.org/10.2354/psj.16.1>).
- 901 128. Warren Y, Williamson EA. 2004 Transport of dead infant mountain gorillas by mothers

- 902 and unrelated females. *Zoo Biol.* **23**, 375-378. (<https://doi.org/10.1002/zoo.20001>).
- 903 129. Biro D, Humle T, Koops K, Sousa C, Hayashi M, Matsuzawa T. 2010 Chimpanzee
904 mothers at Bossou Guinea carry the mummified remains of their dead infants. *Curr.*
905 *Biol.* **20**, 351-352. (<https://doi.org/10.1016/j.cub.2010.02.031>).
- 906 130. Nakagawa N. 2007 *The running monkeys of the Savanna: ecology and society of*
907 *Patas monkeys*. Kyoto: Kyoto University Press. (in Japanese).
- 908 131. Lu, JQ, Zhao DP, Li BG. 2007 Prolonged carrying of a dead infant among the golden
909 monkey (*rhinopithecus roxelanna*) in the Qinling Mountains, China. *Acta Zool. Sinica.*
910 **53**, 175-178. (Chinese with English Summary).
- 911 132. Fashing PJ, Nguyen N, Barry TS, Goodalle CB, Burke RJ, Jones SCZ, Kerby JT, Lee
912 LM, Nurmi NO, Venkata VV. 2011 Death among geladas (*Theropithecus gelada*): a
913 broader perspective on mummified infants and primate thanatology. *Am. J. Primatol.*
914 **73**: 405-409. (<https://doi.org/10.1002/ajp.20902>).
- 915 133. Watson C. Hashimoto N. Takayoshi N. Okamoto N. Matsuzawa T. 2015 Two cases of
916 dead infant carrying followed by mother infant cannibalism in captive socially housed
917 Japanese macaques. *Folia Primatol.* **86**, 378-379.
918 (https://doi.org/10.14907/primate.31.0_76_1).
- 919 134. Sugiyama Y, Kurita H, Matsui T, Kimoto S, Shimomura T. 2009 Carrying of dead
920 infants by Japanese macaque (*Macaca fuscata*) mothers. *Anthropol. Sci.* **117**, 113–119.
921 (<https://doi.org/10.1537/ase.080919>).
- 922 135. van Lawick-Goodall J. 1968 The behaviour of free-living chimpanzees in the Gombe
923 Stream Reserve. *Anim.Behav. Monogr.* **1**, 161-311. ([https://doi.org/10.1016/S0066-](https://doi.org/10.1016/S0066-1856(68)80003-2)
924 [1856\(68\)80003-2](https://doi.org/10.1016/S0066-1856(68)80003-2)).
- 925 136. Green S. 1975 Variation of Vocal Pattern with Social Situation in the Japanese Monkey
926 (*Macaca fuscata*): a field study. In *Primate Behavior: Developments in Field and*
927 *Laboratory Research*, Vol. 4, Rosenblum LA. (Ed). pp. 1-102. New York: Academic
928 Press.
- 929 137. Rajpurohit LS. 1997 Why do mothers carry the corpses of their infants in Hanuman
930 langurs, *Presbytis entellus*. *J. Nat. Con.* **9**, 183–193.
- 931 138. Cheney DL. Seyfarth RM. 2007 *Baboon metaphysics: The evolution of a social mind*.

- Chicago: University of Chicago Press.
139. Biro, D. 2011 Chimpanzee mothers carry the mummified remains of their dead infants: Three case reports from Bossou. In: T. Matsuzawa, T. Humle & Y. Sugiyama (Eds.) *The Chimpanzees of Bossou and Nimba*, pp. 241-250. Tokyo: Springer Verlag. (https://doi.org/10.1007/978-4-431-53921-6_26).
 140. Boesch C. 1991 The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*. **117**, 220-241. (<https://doi.org/10.1163/156853991X00544>).
 141. Mori A, Iwamoto T, Bekele A. 1997 A case of infanticide in a recently found gelada population in Arsi, Ethiopia. *Primates*. **38**, 79-88. (<https://doi.org/10.1007/BF02385924>).
 142. Boesch C. Boesch-Achermann H. 2000 *The chimpanzees of the Tai Forest: Behavioural ecology and evolution*. Oxford University Press, USA.
 143. Bezerra BM, Keasey MP, Schiel N, da Silva Souto A. 2014 Responses towards a dying group member in a wild New World Monkey. *Primates*. **55**, 185-188. (<https://doi.org/10.1007/s10329-014-0412-8>).
 144. Cronin KA, van Leeuwen, EJC, Mulenga, IC, Bodamer MD. 2011 Behavioral response of a chimpanzee mother toward her dead infant. *Am. J. Primatol.* **73**, 415-421. (<https://doi.org/10.1002/ajp.20927>).
 145. Allen C, Hauser MD. 1991 Concept attribution in nonhuman animals: theoretical and methodological problems in ascribing complex mental processes. *Philos. Sci.* **58**, 221-240. (<https://doi.org/10.1086/289613>).
 146. Palombit RA, Seyfarth RM, Cheney DL. 1997 The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Anim. Behav.* **54**, 599-614.
 147. Hart BL, Hart LA, Pinter-Wollman N. 2008 Large brains and cognition: where do elephants fit in?. *Neurosci. Biobehav. Rev.* **32**, 86-98. (<https://doi.org/10.1016/j.neubiorev.2007.05.012>).
 148. Moss C. 1988 *Elephant Memories: Thirteen Years in the Life of an Elephant Family*. New York: William Morrow & Co.
 149. Poole J. 1996 *Coming of age with elephants: A memoir*. New York: Hyperion Press.
 150. Payne KB. 2003 Sources of social complexity in the three elephant species. In: *Animal social complexity: intelligence, culture, and individualized societies*. De Waal FBM,

- 962 Tyack PL. (Eds.). Cambridge, Massachusetts: Harvard University Press.
- 963 151. Douglas-Hamilton I, Bhalla S, Wittemyer G, Vollrath F. 2006 Behavioural reactions of
 964 elephants towards a dying and deceased matriarch. *Appl. Anim. Behav. Sci.* **100**,87–
 965 102. (<https://doi.org/10.1016/j.applanim.2006.04.014>).
- 966 152. Bere R. 1966 *The african elephant*. New York: Golden Press.
- 967 153. Sikes S. 1971 *The natural history of the african elephant*. London: Weidenfeld and
 968 Nicholson
- 969 154. Safina, C., 2015 *Beyond Words: What Animals Think and Feel*. Henry Hold & Co.
- 970 155. Boesch C., 2012 *Wild Cultures: a comparison between chimpanzee and human*
 971 *cultures*. Cambridge: Cambridge University Press.
- 972 156. Buss IO. 1990 *Elephant Life. Fifteen years of High Population Density*. Ames: Iowa
 973 State University Press.
- 974 157. Grzimek B. 1956 Ein merkwürdiges Verhalten von afrikanischen Elefanten. *Ethology*,
 975 **13**, 151-152.
- 976 158. Merte CE, Gough KF, Schulte BA. 2008 Investigation of a fresh African elephant
 977 carcass by conspecifics. *Survival*. **46**, 124-126
- 978 159. Spinage CA. 1994 *Elephants*. London: T & AD Poyser.
- 979 160. McComb K. Baker L. Moss C. 2006 African elephants show high levels of interest in the
 980 skulls and ivory of their own species. *Biol. Letters*. **2**, 26-28.
 981 (<https://doi.org/10.1098/rsbl.2005.0400>).
- 982 161. McComb K. Moss C. Sayialel S. Baker L. 2000 Unusually extensive networks of vocal
 983 recognition in African elephants. *Anim. Behav.* **59**, 1103-1109.
 984 (<https://doi.org/10.1006/anbe.2000.1406>).
- 985 162. Reggente MA, Alves F, Nicolau C, Freitas L, Cagnazzi D, Baird RW, Galli P. 2016
 986 Nurturant behaviour toward dead conspecifics in free-ranging mammals: new records
 987 for odontocetes and a general review. *J. Mammal.* **97**, 1428–1434.
 988 (<https://doi.org/10.1093/jmammal/gyw089>).
- 989 163. Mann J, Barnett H. 1999 Lethal tiger shark (*Galeocerdo cuvieri*) attack on bottlenose
 990 dolphin (*Tursiops* sp.) calf: defence and reactions by the mother. *Mar. Mamm. Sci.* **15**,
 991 568–575. (<https://doi.org/10.1111/j.1748-7692.1999.tb00823.x>).

- 992 164. Quintana-Rizzo E, Wells RS. 2016 Behaviour of an adult female bottlenose dolphin
 993 (Tursiops truncatus) toward an unrelated dead calf. *Aquat. Mamm.* **42**,198–202.
 994 (<http://dx.doi.org/10.1578/AM.42.2.2016.198>).
- 995 165. Dudzinski KM, Sakai M, Masaki K, Kogi K, Hishii T, Kurimoto M. 2003 Behavioral
 996 observations of adult and sub-adult dolphins towards two dead bottlenose dolphins
 997 (one female and one male). *Aquat. Mamm.* **29**,108–116.
- 998 166. Whitehead H. Rendell L. 2014 *The cultural lives of whales and dolphins*. Chicago:
 999 University of Chicago Press.
- 1000 167. Cozzi B, Huggenberger S, Oelschläger HA 2017 *Anatomy of dolphins: Insights into*
 1001 *body structure and function*. Amsterdam: Elsevier.
- 1002 168. Muller Z. 2010 The curious incident of the giraffe in the night time. *Giraffa Newsl* **4**, 20 –
 1003 23.
- 1004 169. Carter K. 2011 Interesting giraffe behavior in Etosha National Park. *Giraffa Newsl*. **5**, 14
 1005 –15.
- 1006 170. Strauss MK, Muller Z. 2013 Giraffe mothers in East Africa linger for days near the
 1007 remains of their dead calves. *Afr. J. Ecol.* **51**506–9. (<https://doi.org/10.1111/aje.12040>).
- 1008 171. Bercovitch FB. 2012 Giraffe cow reaction to the death of her newborn calf. *Afr. J. Ecol.*
 1009 **51**, 376–379. (<https://doi.org/10.1111/aje.12016>).
- 1010 172. Kenyon KW. 1969 Sea otter in eastern Pacific Ocean. *North Am. Fauna*. **68**,1–352.
- 1011 173. Appleby R. Smith B.Jones D. 2013 Observations of a free-ranging adult female dingo
 1012 (Canis dingo) and littermates' responses to the death of a pup. *Behav. Proc.* **96**, 42–46.
 1013 (<https://doi.org/10.1016/j.beproc.2013.02.016>).
- 1014 174. Allen S. 1980 Notes on the births and deaths of harbor seal pups at Double Point,
 1015 California. *The Murrelet*. **61**, 41–43.
- 1016 175. Rosenfeld M. 1983 Two female northwest Atlantic harbor seals (*P. vitulina concolor*)
 1017 carry dead pups with them for over two weeks - some unusual behavior in the field and
 1018 its implication for a further understanding of maternal investment. Abstract, pp. 87, in
 1019 the 5th Biennial Conference on Biology of Marine Mammals, Boston, MA.
- 1020 176. Austin KS, Bohorquez A, Grigg E. Green D, Allen S, Markowitz H. 2001 Observations
 1021 of epimeletic behavior in northern Pacific harbor seal mothers toward their dead pups

- 1022 at Castro Rocks, San Francisco Bay, California. Abstract, pp. 12, in the 14th Biennial
1023 Conference on the Biology of Marine Mammals,, Vancouver, Canada.
- 1024 177. Hartman DS. 1979 Ecology and behavior of the manatee (*Trichechus manatus*) in
1025 Florida. Special Publication No.5. *Am. Soc. of Mammal.* Pittsburgh, Pennsylvania.
- 1026 178. Sol D. 2009 Revisiting the cognitive buffer hypothesis for the evolution of large brains.
1027 *Biol. Letters.* **5**, 130-133. (<https://doi.org/10.1098/rsbl.2008.0621>).
- 1028 179. van Horik , Emery NJ. 2011 Evolution of cognition. *Wires Cogn. Sci.* **2**, 621-633.
1029 (<https://doi.org/10.1002/wcs.144>).
- 1030 180. Kagan J. 2009 Categories of novelty and states of uncertainty. *Rev. Gen. Psychol.* **13**,
1031 290. (<https://doi.org/10.1037/a0017142>).
- 1032 181. Maren S. 2014 Fear of the unexpected: hippocampus mediates novelty-induced return
1033 of extinguished fear in rats. *Neurobiol. Learn. Mem.* **108**, 88-95.
1034 (<https://doi.org/10.1016/j.nlm.2013.06.004>).
- 1035 182. Balderston NL, Schultz DH, Helmstetter FJ. 2013 The effect of threat on novelty
1036 evoked amygdala responses. *PloS One.* **8**, e63220.
1037 (<https://doi.org/10.1371/journal.pone.0063220>).
- 1038 183. Rosen JB, Donley MP. 2006 Animal studies of amygdala function in fear and
1039 uncertainty: relevance to human research. *Biol. Psychol.* **73**, 49-60.
1040 (<https://doi.org/10.1016/j.biopsycho.2006.01.007>).
- 1041 184. Mori M, MacDorman KF, Kageki N. 2012 The uncanny valley [from the field]. *IEEE*
1042 *Robot. Autom. Mag.* **19**, 98-100. (<https://doi.org/10.1109/MRA.2012.2192811>).
- 1043 185. Piwek L, McKay LS, Pollick FE. 2014 Empirical evaluation of the uncanny valley
1044 hypothesis fails to confirm the predicted effect of motion. *Cognition.* **130**, 271-277.
1045 (<https://doi.org/10.1016/j.cognition.2013.11.001>).
- 1046 186. Fox R, McDaniel C. 1982 The perception of biological motion by human infants.
1047 *Science.* **218**,486-487. (<https://doi.org/10.1126/science.7123249>).
- 1048 187. Cross DJ. Marzluff JM. Palmquist I. Minoshima S. Shimizu T. Miyaoka R. 2013 Distinct
1049 neural circuits underlie assessment of a diversity of natural dangers by American
1050 crows. *Proc. R. Soc. B.* **280**, 20131046. (<https://doi.org/10.1098/rspb.2013.1046>).
- 1051 188. Mori M. 1970. The uncanny valley. *Energy.* **7**, 33-35.

- 1052 189. Kätsyri J, Förger K, Mäkäpäinen, M., & Takala, T. 2015. A review of empirical evidence
1053 on different uncanny valley hypotheses: support for perceptual mismatch as one road
1054 to the valley of eeriness. *Front. Psychol.* **6**, 390.
1055 (<https://doi.org/10.3389/fpsyg.2015.00390>).
- 1056 190. Goodall J. 1986 Social rejection, exclusion, and shunning among the Gombe
1057 chimpanzees. *Evol. Hum. Behav.* **7**, 227-236. ([https://doi.org/10.1016/0162-](https://doi.org/10.1016/0162-3095(86)90050-6)
1058 3095(86)90050-6).
- 1059 191. MacDorman KF, Ishiguro H. 2006 The uncanny advantage of using androids in
1060 cognitive and social science research. *Interact. Stud.*, **7**, 297–337.
1061 (<https://doi.org/10.1075/is.7.3.03mac>).
- 1062 192. MacDorman KF, Green RD, Ho CC, Koch CT. 2009 Too real for comfort? Uncanny
1063 responses to computer generated faces. *Comput. Hum. Behav.* **25**, 695–710.
1064 (<https://doi.org/10.1016/j.chb.2008.12.026>).
- 1065 193. Steckenfinger SA, Ghazanfar AA. 2009 Monkey visual behavior falls into the uncanny
1066 valley. *Proc. Nat. Acad. Sci.* **106**, 18362-18366.
1067 (<https://doi.org/10.1073/pnas.0910063106>).
- 1068 194. Lewkowicz DJ, Ghazanfar AA. 2012 The development of the uncanny valley in infants.
1069 *Dev. Psychobiol.* **54**, 124-132. (<https://doi.org/10.1002/dev.20583>).
- 1070 195. Spelke ES. Kinzler KD. 2007 Core knowledge. *Dev. Sci.* **10**, 89–96.
1071 (<https://doi.org/10.1111/j.1467-7687.2007.00569.x>).
- 1072 196. Santos LR. Hughes KD. 2009 Economic cognition in humans and animals: the search
1073 for core mechanisms. *Curr. Op. Neurobiol.* **19**, 63-66.
1074 (<https://doi.org/10.1016/j.conb.2009.05.005>).
- 1075 197. Carey S. 2009 *The Origin of Concepts*. New York: Oxford University Press.
- 1076 198. Hebb DO. 1946 On the nature of fear. *Psychol. Rev.* **53**, 259-276.
1077 (<http://dx.doi.org/10.1037/h0061690>).
- 1078 199. Boyer P. 2001 *Religion explained: The evolutionary origins of religious thought*. New
1079 York: Basic books.
- 1080 200. Pettitt P. 2011 *The Palaeolithic origins of human burial*. London: Routledge.
- 1081 201. Barrett HC. Behne T. 2005 Children's understanding of death as the cessation of

- 1082 agency: a test using sleep versus death. *Cognition*. **96**, 93-108.
 1083 (<https://doi.org/10.1016/j.cognition.2004.05.004>).
- 1084 202. White C. Fessler DM. Gomez PS. 2016 The effects of corpse viewing and corpse
 1085 condition on vigilance for deceased loved ones. *Evol. Hum. Behav.* **37**, 517-522.
 1086 (<https://doi.org/10.1016/j.evolhumbehav.2016.05.006>).
- 1087 203. Butler R, 1964 The reactions of rhesus monkeys to fear-provoking stimuli. *J. Gen.*
 1088 *Psychol.* 104,321-330. (<https://doi.org/10.1080/00221325.1964.10532568>).
- 1089 204. Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier R R, Seyfarth RM, Cheney
 1090 DL. 2006 Behavioural and hormonal responses to predation in female chacma
 1091 baboons (*Papio hamadryas ursinus*). *Proc. R. Soc. B.* **273**, 707–712.
 1092 (<https://doi.org/10.1098/rspb.2005.3378>).
- 1093 205. Melland F. 1938 Elephants in Africa. Country Life.
 1094