

Opinion piece



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Behaviour of nonhuman primate mothers toward their dead infants: uncovering mechanisms

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In comparative thanatology, most reports for nonhuman mammals concern mothers' behavioural responses to their dead offspring: most prominently, dead-infant carrying (sometimes of extended duration); but also inspection, proximity, maternal care such as grooming, protective behaviours and filial cannibalism. Documented across many primate species, these behaviours remain poorly understood in all. The literature is dominated by relatively brief qualitative descriptions of isolated anecdotal cases in apes and monkeys. We argue for quantitative coding in case reports, alongside analyses of longitudinal records of such events to allow objective evaluation of competing theories, and systematic comparisons within and across species and populations. Obtaining necessary datasets depends on raised awareness in researchers of the importance of recording occurrences and knowledge of pertinent data to collect. We review proposed explanatory hypotheses and outline data needed to test each empirically. To determine factors influencing infant-corpse carriage, we suggest analyses of deaths resulting in 'carry' versus 'no carry'. For individual cases, we highlight behavioural variables to code and the need for hormonal samples. We discuss mothers' stress and welfare in relation to infant death, continued transportation and premature removal of the corpse. Elucidating underlying proximate and ultimate causes is important for understanding phylogeny of maternal responses to infant death.

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

1. Introduction: How do mothers behave towards their dead infants?

In the emerging discipline of comparative thanatology, most reports for nonhuman mammals concern mothers' behavioural responses to their dead offspring, continued transportation being most evident. Mothers may carry the corpse of their infant for hours, days or months—sometimes after all resemblance to a living infant ceases, beyond bloating and mummification, clutching only skeletal remains or a disintegrated fragment. Extended duration carrying is not exceptional (table 1). Most commonly, however, transportation lasts between one and several days, and mothers typically direct caretaking behaviour to the dead infant as if it were still alive, such as grooming and apparently protective behaviours. Despite reports across a diverse array of species, both captive and wild, from apes, monkeys and manatees to dolphins and dingoes [2,17,18,21], this striking phenomenon remains poorly understood. Proximity after death and 'inspecting' the infant-corpse are seen even more broadly across taxa (e.g. in giraffes, table 1). Elucidating underlying proximate and ultimate causes is an important requirement for understanding the phylogeny of maternal responses to death in infants.

Table 1. Range of dead infant-directed behaviours observed across taxa: selected individual examples. Behaviours are as reported by authors of the respective papers. Note that the absence of a tick does not necessarily mean that the behaviour did not occur, only that it was not reported. Duration of carry (days) relates to one particular individual case.

category	species	infant-corpse directed behaviour by mother										references	captive (c); wild (w); provisioned free-ranging (f); rehabilitant (r)			
		duration in proximity to corpse (if no carry)	approach/ retreat repeatedly	peer	sniff	lick	touch-inspect with hand/fin	groom	hold/carry	duration of carry (days)	cannibalism			swat	wasp/fly	block crows
				investigate	caretaking	other	protect/defend									
apes	chimpanzee ^a	—	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[1]	w
		—	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[2]	w
	bonobo ^b	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[3]	c, r
		—	—	—	—	—	—	—	—	—	—	—	—	—	[4]	w
monkeys (Old World)	orangutan ^c	—	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[5]	w
	gorilla ^d	—	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[6]	f, r
	Japanese macaque ^e	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[7]	w
	Taihangshan macaque ^f	—	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[8,9]	c
monkeys (New World)	macaque ^g	—	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[10]	f
	Tonkean macaque ^h	—	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[11]	c
	Yunnan snub-nosed monkey ⁱ	—	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[12]	w
	capuchin monkey ^k	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[13]	f
prosimian	ring-tailed lemur ^l	~6 hr	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[14]	f	
cetacean	Risso's dolphin ^m	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[15]	w	
canid	Dingo ⁿ	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[16]	w	
ungulate	Rothchild's giraffe ^o	3 days	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[17]	w	
	Thomicroft's giraffe ^p	2 hr	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[18]	w	
		—	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[19]	w	
		—	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	[20]	w	

^a*Pan troglodytes*; ^b*P. paniscus*; ^c*Pongo abelii*; ^d*Gorilla beringei beringei*; ^e*Macaca fasciata fasciata*; ^f*M. mulatta chelensis*; ^g*M. tonkeana*; ^h*Theropithecus betsi*; ⁱ*Semnopithecus entellus*; ^j*Rhinopithecus bieti*; ^k*Cebus capuchinus*; ^l*Lemur catta*; ^m*Grampus griseus*; ⁿ*Rhinopithecus bieti*; ^o*Giraffa camelopardalis rothschildii*; ^p*G. c. thomicrofti*; ^qfour confirmed instances of transporting corpse; ^r'others' refers to conspecifics, humans, boats; [±] unknown.

The currently available literature is dominated by relatively brief, qualitative descriptions of isolated, anecdotal cases. Remarkably, despite hundreds of reported instances of dead-infant care and portage, virtually none include quantitative coding of behavioural responses. Further, only one study has analysed longitudinal records of multiple cases [22], leaving a major source of potential insight unexplored.

Why is it necessary to take a quantitative approach? With qualitatively similar behaviours seen across taxa in response to infant death, quantitative data will enable direct systematic comparisons between as well as within species and across populations. Mothers' response to their dead infant is a highly emotive topic; therefore, conclusions based on objective, quantitative evidence are of particular importance. In seeking to understand behavioural responses to infant death, we must avoid both over-interpretation and speculation as much as under-interpretation, and define often-loaded terms like 'grieve' and 'mourn' operationally. Most fundamentally, quantitative evidence will be necessary to reveal causal mechanisms, to allow us to test proposed theories empirically.

We cannot yet explain why some mothers abandon their infant soon after it dies, but others continue carriage for weeks. Why do mothers carry at all? What causes carrying of extended duration, followed by eventual discard? It is sometimes assumed that strength of the maternal–infant bond alone underlies transport and care of the infant-corpse, especially for animals with complex cognitive capacity, but influencing factors are likely to be numerous and complicated. Several researchers have highlighted the need to consider alternative explanations, such as climate [12]. Furthermore, extended carrying is seen in a wide variety of Old World primates (table 1) [12]. Intriguingly, both monkey and ape mothers have been observed to perform behaviours of opposite extremes toward their infant-corpse: both protective, nurturant care and carrying, and cannibalism (table 1). Strikingly, carrying can overlap cannibalism. One monkey mother carried her dead infant for a further three days after cannibalizing [8,9] with no further cannibalism events subsequently observed. Any explanatory theory must account for such apparently contradictory behaviours.

Many hypotheses for post-mortem attentive behaviours towards infants have been put forward and discussed [21]; however, the literature generally lacks explicit suggestions for testing such hypotheses directly. Focusing on nonhuman primates, we review the proposed hypotheses and delineate the data that will be required for systematic analyses of contributing factors. For case reports, we outline variables to be coded quantitatively, and discuss stress in relation to infant death, carrying and early removal of the corpse. Although our review concerns mainly nonhuman primates, much of the discussion and many suggested quantitative measures are equally applicable to a wider range of taxa. We focus on mothers' responses to infant death (not sick or dying infants or adult death) and observational not experimental approaches (e.g. [23]).

2. Possible explanations

Care towards and carriage of dead infants have generated considerable interest and speculation across several disciplines. To uncover underlying mechanisms, we must consider all existing hypotheses, generate additional interpretations,

examine evidence for and against and accumulate quantitative data for empirical evaluation. Hypotheses are listed in table 2, with the quantitative data needed to test each. Consideration of influencing factors should ideally be driven by predictive theory. While some hypotheses stand in direct opposition, other sets of hypotheses may not be mutually exclusive.

Continued maternal care and carrying following the death of an infant have been interpreted as a direct index of maternal-bond strength [2,14]. However, distinguishing this measure from related variables, including disentangling mothers' emotional from biological investment, presents challenges. Potential hormonal influence has been highlighted, with authors suggesting that pregnancy hormones underlie post-partum attentive behaviours [7,24] and that resumption of cycling leads to discarding the corpse [2]. It is unlikely that maternal affection represents the sole underlying cause across all taxa for at least three reasons, outlined below.

First, nurturant care and/or dead-infant carrying are in some instances combined with [4,5,10] and, importantly, may even overlap, the mother ingesting flesh or dried flesh from the corpse, with careful carrying resumed afterward for hours to days [6,8,9,11]. The juxtaposition of care and cannibalism is puzzling. For example, a wild bonobo mother groomed her infant-corpse immediately before cannibalizing it [4]. If cannibalism always occurred at the end of carrying, immediately before discard of the corpse, this would be consistent with a gradual weakening of the mother–infant bond, from treating it as if alive (grooming, protecting and carrying it) to treating the body eventually as an object/food. The incidence of overlap, continued carrying after cannibalizing, suggests simultaneous, conflicting impulses. If carrying behaviour is driven purely by maternal affection, it is difficult to explain recommencement of carrying after eating part of the corpse. Although cannibalistic mothers may simply be carrying around an easy source of food, this interpretation seems unlikely because of the apparent care with which they carry it, the length of time that is probably energetically costly and the lack of subsequent cannibalism or further missing fragments observed before discard. Elucidating what drives the maternal cannibalism element, considered a natural behaviour, could help to unlock the motivations underlying the phenomenon of dead-infant carrying.

Second, corpse-carrying and care are not limited to mothers, or even to females, and it extends across species boundaries. Other females within a group may carry the infant-corpse (gorilla: [7]; gelada baboon: [12]); even females of a different group [12]. Dead-infant transportation and care by males can be explained by neither maternal bond nor hormones. A male bonobo carried, protected and groomed the body of his dead sister [25]; a rhesus monkey behaved similarly toward an adopted infant for a day after it died [26]; a baboon carried the corpse of an infant killed during a fight for a week [27]. Such behaviour is perhaps less surprising for species in which males are heavily involved with infant care and thus social bonds between males and infants may be formed pre-death. Male barbary macaques (*Macaca sylvanus*) of all age categories carry, protect and groom dead infants, using them in species-typical social interactions including agonistic buffering [28]. Cases of interspecific corpse care include a female captive guenon monkey inspecting, grooming and carrying a dead rat for two days [27]. Most

Table 2. Potential explanations for mothers' behavioural responses to dead infants and the data required to test each empirically.

category	hypotheses	ref.	data required
mother	maternal-bond strength	[1,2,11,14,16,24]	proximity to corpse over time [3,8,9]; effect of age of infant at death (time to bond)
	post parturition hormones	[2,7,24]	hormone metabolite levels in urine/faeces (prolactin, oxytocin): pre-mortem and post-mortem (compare for 'carry'/'no carry' mothers), during carrying and after discard (for 'carry' mothers), association with frequency/duration of nurturant behaviours; compare: carrying rate, 'carry' versus 'no carry', for infants dying within period of hormonal influence versus dying older, stillborn versus dying ≥ 1 day old; observe when cycling resumes relative to discard
	'unawareness' of death	[13,22,24]	submersion of corpse in water [21]; experimental approaches
	lack of experience with dead individuals	[22]	number of dead individuals interacted with in lifetime prior to dead infant: 'carry'/'no carry', behavioural responses observed
	learning about death	[3]	quantitative coding of inspection behaviours/sensory cues, especially directed to face/head [3]; does likelihood of inspection decrease with higher frequency of previous inspection events?
	'learning to mother'	[7,24]	primiparity; number of previous successfully reared infants; age of mother at infant death; record of nulliparous females interacting with dead infants: subsequent rearing success versus that of comparable nulliparous females without such interaction; do females handle others' dead infants while pregnant? (hormonal influence); quantitative coding of nurturant behavioural responses observed
	maternal experience	[2]	primiparity; number of previous successfully reared infants
	mothers' age at infant death	[13,22]	age of mother at infant death
	'wait and see' strategy	[13,18,24]	primiparity; number of previous successfully reared infants; age of mother at death
	individual differences	this paper	longitudinal records: repeat carries by same individual; carrying durations between and within individuals; measures of individual differences: 'personality', reaction norms in relation to 'carry'/'no carry' and type of behavioural responses observed
	social facilitation	[a]	number of mothers in same group carrying live infants at time of infant death: 'carry'/'no carry'
	cultural transmission	[2]	number of other mothers in same group carrying dead infants in lifetime of mothers that 'carry'/'no carry'; evidence for social learning (gaze orientation/observation)
	costly signalling of maternal diligence ^c	[b]	relative reproductive success/quality of males copulated with: for females of comparable age, parity and rank (etc.) for females that have carried versus have not; coding of gaze orientation of males toward females carrying dead infant (evidence of selective attending)
	social rank	this paper	social rank of mother; social network analysis
	dead-infant carrying mitigates stress in mother ^c	this paper	glucocorticoid levels and negative behavioural indicators observed (stress-related, 'depressive'): pre-mortem and post-mortem (compare for 'carry'/'no carry' mothers), during carry and after discard (for carry mothers)
	parallels to species-specific infant developmental stage	([22], this paper)	age of infant at death in relation to species-specific developmental stages
	species differences in handling dead infants of different sexes	this paper	sex of infant—'carry'/'no carry', carrying duration, behavioural responses observed for various species in relation to species-specific differences in relating to live infants of different sexes

(Continued.)

Table 2. (Continued.)

category	hypotheses	ref.	data required
infant	age at death	[14,22]	age of infant at death; developmental stage at death
	sex	[22]	sex of infant
	morphological resemblance to live infant ^c	[11] ^d	over time: % body remaining; objective rating state of corpse over time, carrying duration
	cause/context of death: (traumatic versus 'peaceful')	[21]	cause of infant death (peaceful: perinatal death, disease; traumatic: death from injury, infanticide)
ecological/ environmental factors	extreme climatic conditions	[12,21 ^d][5 ^d]	seasonal influence—climatic conditions: rainfall, humidity, temperature, season; comparisons across various climates [21] – 'carry'/'no carry', carrying duration
	slow decomposition ^c		
	arboreality ^c	[21]	population carrying rates, carrying durations: in arboreal/non-arboreal species; frequency corpse dropped from trees/height; comparisons across various terrain difficulty
	demands of foraging ^c	[22] ^d	compare provisioned populations versus non-provisioned: carrying durations

^aJR Anderson 2015, personal communication.

^bCP Van Schaik 2015, personal communication

^cRelates to dead-infant carrying and carrying duration only.

^dRelates to carrying duration only.

strikingly, a post-menopausal wild female bonobo groomed, protected and carried a dead red-tailed monkey for 43 days, latterly only a skeleton [29]. These latter cases suggest that carrying and nurturant behaviour towards a corpse is not dependent on pre-mortem bond formation. This also applies to tending, carrying and extended carrying by mothers of stillborn infants [30], though hormonal factors may influence such responses.

Third, if maternal-bond strength alone determined carrying, presumably infants surviving longer prior to death, allowing more time for mothers to form a strong bond, would more likely be carried than those dead soon after birth [14,31]. However, longitudinal evidence indicates the converse [22]. In a pioneering study systematically assessing three influencing factors (mothers' age, infant age and sex) in a population of Japanese macaques over 9 years, 80% of carried infant-corpse died within 30 days of birth. Further, mothers carried less than 5% of infants that died between 31 and 253 days old. When considering influence of infant age at death, predictions should correspond to biologically meaningful infant developmental stages. In Japanese macaques, 30 days coincides with a transition from high to lower dependency; from travelling while clinging to their mother and getting pulled back/retrieved if they wander, to following behind more independently [22]. If maternal behaviour to infant-corpse is interpreted as a continuation from pre-morbid tendencies [22], we might expect infants dying at a stage of relatively higher dependency as more likely to be carried, and similarly kept close, by their mothers in death as in life.

For perinatal infant deaths, any hormonal influences (oxytocin, prolactin) on behavioural responses to the infant-corpse are likely to be particularly potent, with primates predisposed to mothering behaviour in the last few weeks of pregnancy [7,24]. Intriguingly, Sugiyama *et al.* [22] found that 90% of Japanese macaque infants that died one day (and no longer) after birth were carried versus less than a

quarter of infants that died within a day of birth (or were stillborn). This suggests that handling the infant alive may be an important precursor for hormonal effects to initiate carrying and nurturant behaviour. Perhaps when cycling later resumes the mother continues to transport the corpse, but 'views' the infant-corpse differently. This further underlines the need for hormonal sampling. However, increased time for bonding may still be a predictor among mothers whose infants die above a certain age, e.g. without influence of perinatal/lactation hormones.

An intuitive assumption is that mothers must recognize their infant as dead due to the lack of response when they direct behaviour toward it. However, this is difficult to establish with any certainty. In fact, one explanation for continued care and carriage rests on the opposite assumption, that mothers do not 'realize' the infant is dead [22], instead considering it unconscious/unanimated [24]. Perhaps females inexperienced as mothers or at encountering dead individuals are more likely 'confused' and so more likely to carry than more experienced mothers [22]. Indeed, apparent 'grief' may be difficult to distinguish operationally from possible 'confusion'. Inspection by a chimpanzee mother of her dead infant has been interpreted as potentially gaining sensory cues, leading to learning about death [3]. Some authors have suggested that nulliparous females may be predisposed to handle dead infants to learn mothering skills [7,24]. This may extend to some inexperienced mothers, for example, if their first infant is stillborn or has died at an early age, whether handling their own dead infant or another's. Females that handle infant corpses potentially increase the likelihood of future offspring surviving through infancy. Although handlers may include females other than the dead infant's mother, if they are kin, 'allowing' others to hold the corpse may increase her inclusive fitness. Common to all these explanations is the expectation that younger, inexperienced mothers and females are more likely to carry the infant-corpse than experienced mothers;

however, these various interpretations should be distinguishable according to the identity of the females handling the dead infant and the types of behaviours observed. For example, if nulliparous females are most motivated to handle the corpse, showing mainly maternal behaviours, then the learning-to-mother hypothesis would be supported, whereas a high frequency of behavioural responses to gain sensory cues would suggest individuals are handling the corpse to learn about death.

Other authors have made the opposite suggestion that more experienced mothers are more likely to carry, and for longer, than inexperienced [2], or that older mothers will carry their dead infant for longer than younger mothers [13]. Inconsistent with the former hypothesis are extended carries by primiparous mothers [8,9,11] and the fact that almost a third of carriers were primiparous in the longitudinal study of Japanese macaques [22]. Further, the same study found no influence of mothers' age on likelihood or duration of carrying [22]. Rather than treating parity as dichotomous, a continuous measure such as number of infants previously reared successfully by a given individual would allow a more fine-grained evaluation, for sufficiently large datasets.

Evolutionary thanatology must include consideration of ultimate function. It may be adaptive to continue carrying and caring for an immobile infant, 'just in case' it is still alive, given the heavy biological investment already made [18,24]. However, carrying is energetically costly, more so the older and heavier the infant [22], and extended carrying is potentially maladaptive [18,22]. Presumably, there is a trade-off between discarding too soon and holding on too long. Further, if carrying delays resumption of cycling, or impedes copulation, it might adversely affect reproductive success. However, carrying an infant-corpse does not preclude copulation; indeed, a chimpanzee mother that copulated while carrying her dead infant showed visual signs of cycling [1] and subsequently gave birth, indicating that she had been fertile during corpse-carriage. A mother gelada baboon copulated frequently two weeks before discarding the corpse [12], indicating that hormonal changes leading to cycling are not sufficient to end carrying [12,31]. Another possible way in which dead-infant carrying may increase fitness indirectly, relevant only in species where there is some sort of partner choice, is that females might 'use' carrying to show males they are skilled, 'good' mothers (CP van Schaik 2015, personal communication). Such females would potentially gain access to a better quality male and improve their reproductive success, although depending on males' perception of the situation, the opposite may be true: a mother investing time and energy into a dead infant may indicate inexperience.

Ecological factors may also exert an influence on dead-infant carrying. That extremes of climate (arid, cold) might delay decomposition making carrying more likely, and extend carrying, was proposed initially as an alternative to the maternal-bond hypothesis [12]. Counter to this proposal are multiple reports of extended carrying by mothers in hot, humid, tropical climates (e.g. [6,8,9]), including over 140 infant-corpse carried in the most humid months despite swift putrefaction [22]. Similarly, inconsistent with continued carrying requiring that corpses resemble live infants morphologically, are the many examples of mothers continuing to transport bloated, misshapen corpses, bodies with missing parts or holding only a single body part; for example, an orangutan mother persisted in carrying only the spinal cord

[6]. Arboreality has also been proposed to curtail carrying [21], with the infant-corpse expected to be less likely retrieved upon falling to the ground. Faster decomposition and tree-living may well place an upper bound on carrying duration. However, arboreality does not necessarily prevent dead-infant carrying of extended duration in wild populations. For example, a free-ranging Japanese macaque mother carried her infant-corpse for 30 days, across densely forested terrain, retrieving the corpse repeatedly whenever it fell from the tree (S Matsuoka 2016, personal communication).

Context of death is another proposed influencing factor, with continued caretaking and portage considered more likely and prolonged following a 'peaceful' death, through illness, than a traumatic death through injury or infanticide [21]. Counter-examples demonstrate this is not categorical: two gorilla infants were carried after presumed violent deaths [7]; a wild barbary macaque mother inspected and carried the corpse of her infant killed by a road vehicle [32]; and an adult male Hamadryas baboon carried and tended an infant after killing it [27]. Context of death may be a better predictor for carrying duration compared to predicting whether or not a mother will carry at all.

Repeat carries by the same mother, i.e. for more than one infant death event [2,8,9,11,22], suggest individual differences in the proclivity for the behaviour. In the only longitudinal study [22], 12 Japanese macaque mothers were repeat carriers. One chimpanzee mother carried her dead infants for 27 and 68 days, respectively [2]; a Japanese macaque mother carried and cared for her dead infant for 29 and 28 days on successive births, each time also cannibalizing [8,9]. This raises an intriguing question: do individuals that carry more than once, carry consistently, i.e. at every opportunity? If not, what causes carrying after some deaths yet not others, by the same individual? Do repeat carrying mothers show a consistent pattern, e.g. always carry for extended duration (nominally defined as longer than 10 days [12]); always combine with cannibalism [8,9]? Might these outcomes reflect genetic influence, individual or social learning? Might 'personality' and individuals' reaction norms influence tendency towards particular behavioural responses to dead infants? Do repeat carriers differ from one-time carriers? The longitudinal study of Japanese macaques found no appreciable difference in the ages of repeat carrier mothers or the duration of carrying observed compared with one-time carriers [22]. Importantly, data on repeat carriers might help to clarify the role of (or eliminate) some other factors, such as parity, age and context of death.

It has been suggested that multiple carriers within a social group may be indicative of cultural transmission [2]. Cultural influence might also be evident in the manner, or 'group-style', in which other members respond to dead infants: interest and investigation [2,13] versus no apparent interest [22]. More immediately, social contagion or social facilitation [33] might be a proximate cause of dead-infant carrying. Seeing other mothers in the group holding young (live) infants might motivate a mother to similarly keep holding onto her lifeless infant (JR Anderson 2015, personal communication). This would perhaps be especially likely in species with a fixed birth season and large groups (many mothers carrying at once). Mediating factors might be the total number of other mothers in the group carrying live infants and the degree of association between these individuals and the bereaved mother, with a higher number and stronger association increasing the likelihood of social facilitation.

Social rank of the mother is a potential influencing factor, but as yet unlinked to predictive theory and without indication of a hypothesized direction of difference. Given that carrying is energetically costly, high-ranking mothers may be physically more able to carry for longer, with more access to more and higher quality food, even while still carrying or keeping the corpse in proximity. Conversely, perhaps lower-ranking, more peripheral females will carry the corpse for longer, with fewer baseline social associations. There is scope for application of social network analyses [34].

For other putative contributory factors not yet associated with specific hypotheses, conceivably, species differences in the way mothers relate to their live infants, such as disparity in behaviour according to sex of the infant, may similarly influence responses to dead infants. However, in the longitudinal study of Japanese macaques, no significant difference in the proportion of male and female infant-corpse carried was found [22].

What influence might wild or free-ranging, provisioned versus captive context have on post-partum attentive care, likelihood of continued carrying and carrying duration? Carrying, including extended duration carrying, is seen in all three population types (table 1). Wild populations likely show the highest rate of infant mortality, leading to more opportunities for dead-infant care and carrying but higher energetic costs. Free-ranging, provisioned groups, such as the Takasakiyama group [22], have access to supplementary food, but not veterinary care. Mothers in populations with a poor abundance of food, high foraging demands [22] and a large home range with difficult terrain presumably face the highest energetic costs of continued carrying; extended carrying under such circumstances indicates high underlying motivation. Captive groups inhabit a restricted area, presumably making carrying less energetically taxing, though captive areas may still be relatively large and complex [3,8,9]. None of the observed behaviours by mothers toward their dead infant are considered abnormal (but see [6]).

3. Longitudinal data

Which parameters have explanatory and predictive power for dead-infant carrying behaviour? Long-term datasets of multiple records of mothers' care for and carriage of infant-corpse, from captive and field populations, represent vast potential for elucidating underlying mechanisms. Typically, case reports discuss implications for only a few hypotheses, and risk skew from small sample sizes (e.g. [14]). Longitudinal data will enable systematic evaluation of possible contributing factors (table 2), and multivariate testing. Despite obvious prospective benefits, so far there exists only one set of population-level quantitative analyses for dead-infant carrying [22], indeed for any nonhuman mammalian behavioural response to death. The data come from one population of one species (Japanese macaques). Accumulating longitudinal datasets necessary for future analyses will require wider appreciation of the importance of recording occurrences, alongside awareness of which data to collect to test different hypotheses empirically (table 2). To allow a comprehensive, systematic analysis of potential influencing factors, many relevant variables should be included, along with relevant data on other group members (table 2). At long-term field-sites and for captive populations,

demographic data are already recorded. Collecting additional data on events can be relatively straightforward, provided it is added to the site protocol. As such events are relatively infrequent, collaboration and combining data will be important. Scientists with sufficient foresight may already possess the necessary datasets.

One alternative is meta-analyses of published cases but this may result in missing data points and certainly incomplete data across all factors listed in table 2, as required to test proposed hypotheses empirically. Another important consideration for pooled datasets is careful evaluation of how directly comparable cases are in captive compared to free-ranging, provisioned and wild contexts. Examining potential influences such as parity, individual differences (repeat carriers), social facilitation and social transmission will depend on continuous records of infant-corpse-carrying events within populations over time. So too will calculating carrying rates (number of carrying cases per infant deaths in a population) (after [22]). Importantly, the dataset should include only cases where there was sufficient opportunity for the mother to carry directly following infant death, applicable to both captive conditions and the field. For example, cases of infants stillborn during veterinary intervention or where the infant corpse is removed forcibly from the mother should be excluded. Similarly, carrying duration is invalidated if portage is interrupted artificially or by conspecific intervention.

We suggest a novel approach to analyses—direct comparison of influencing factors between infant deaths after which mothers carry, and deaths after which mothers have the opportunity to carry the corpse yet do not. Note that, due to the infrequent observation of death events and thus limited feasibility of establishing complete absence of carrying, especially in the field, 'no carry' may in fact apply to carrying for no more than a few hours. Effects of multiple potential contributory factors, both nominal and interval level, on the nominal dependent variable (carry/no carry), could be analysed together using logistic regression.

4. Quantitative coding in case reports

(a) Behavioural responses

Case reports could contribute more substantially to this field. Several researchers [3,21] have highlighted the need for more detailed, objective, quantitative data on behavioural responses to death. Behaviours directed by nonhuman primate mothers toward their dead infant include: inspection, proximity, sustained/frequent gaze orientation, continued maternal care, protective behaviours, carrying (sometimes for extended duration), and filial cannibalism (figure 1). Because infant death and mothers' responses cannot be predicted, continued interaction with corpses is observed opportunistically. Most thanatological papers on nonhuman species are contributed by researchers for whom this topic is a side-line. Researchers with a comparative thanatology focus could set out to selectively target populations with high infant mortality, especially those with a high carrying rate, periods of highly expected infant mortality, e.g. birth seasons, and, within such populations and periods, individuals that have previously carried once or repeatedly [8,9]; nonetheless timing remains unpredictable. Scientists, especially in the field [21], should be well prepared in advance to record responses to infant death at

short notice, and have adequate equipment (video camera, spare batteries) and knowledge of which data to collect. Table 3 summarizes pertinent behavioural variables to code quantitatively, those used in previous studies and suggestions for future inclusion.

Conducting observations continuously from infant death to mothers' eventual discard is ideal, yet rarely feasible [22]. Infant death, like birth, is infrequently observed in free-ranging nonhuman primates [22,35]. Researchers quantifying responses in densely vegetated landscapes are limited to windows of time when the mother and infant-corpse are visible; for example, a chimpanzee coming into view as she begins to separate from her dead infant, videoed over a period of 45 min [3]; a carrying mother macaque emerging from thick undergrowth for feeding, videoed for 30–90 min daily over a month [8,9]. Nonetheless, careful coding of even short durations can yield much useful information. Video records enable more detailed coding than can be achieved accurately live; multiple, mutually exclusive measures can be coded for objective comparison. Use of more than one video camera allows different viewpoints, both wide-frame and focused, allowing, for example, coding of both mother's responses to the corpse and proximity/interaction of and with other group members [3]. Videos can be synchronized for simultaneous viewing [3]. Responses of other group members to a dead adolescent [36] and a sub-adult [37] chimpanzee have been coded quantitatively with the help of video records.

Researchers have noted mothers' transition between constant contact with the infant-corpse and discard [3,11,24], but very few have quantified this process. A retreat/approach pattern has been described across several taxa (table 1), with the mother moving away and returning to the corpse repeatedly. Specifically in nonhuman primates, mothers often lay the corpse down to feed, moving further away and for bouts of increasing duration over time. Quantitative coding has been used successfully to track this tendency over minutes (chimpanzee: [3]), hours (lemurs: [16]) and weeks (Japanese macaque: [8,9]).

Infancy is a period associated with high mortality risk, which is partly why reports on responses to dead infants are so numerous. Ideally, coding should take into account species-typical behaviour and proximity of a mother to a live infant of equivalent age. Nonhuman primate infants are dependent on adult care for survival, and are either in constant physical contact with their mother or allo-maternal carer(s), in close proximity or visually monitored. Cronin *et al.* [3] suggested that quantifying mothers' proximity to and gaze orientation toward or away from the infant-corpse offers an objective index of mother–infant bond strength. These represent two important measures to code. They should be interpreted in concert with ad libitum quantitative coding of infant-directed behaviours (table 3) because, for example, like maternal care, episodes of maternal cannibalism also involve close contact/proximity [8,9].

It might be informative to code the mode of carrying over time (table 3). Carrying typically starts off in arms and hands, even when the mother is moving. Later, however, the corpse may be carried in her mouth while she moves [8,9]. Baboon and chimpanzee mothers may carry their dead infant slung across their back [2]. Although live infant monkeys and apes cling, and hence are not usually carried in hands/arms or mouth or across the mother's back as corpses are,

deformed, sick or experimentally anaesthetized infants may be carried in their mothers' arms [22,24].

Inspection of her dead infant by the mother was first coded quantitatively in a chimpanzee mother [3], and later a Japanese macaque [8,9]. Some researchers have noted that mothers selectively direct more attention to the face and/or eyes [3,12,13,27,38] of dead infants. The anal area is also often inspected [15,30]. Because inspection is seen widely across taxa, a comparative approach may be informative especially when combined with reports of inspection of sub-adult (e.g. [37]) and adult corpses.

Importantly, quantitative coding of particular infant-directed behaviours will allow evaluation of proposed hypotheses. For example, whether a mother allows her dead infant to be submerged in water or not may relate to awareness of death [21]. Similarly, protective/defensive behaviour of the infant-corpse, including preventing contact by others, may represent maternal behaviour or 'bereavement-related' behaviour, but this must be distinguished operationally from possessive behaviour towards a 'found' object [39], tool, or corpse of another species. Collecting and analysing hormonal samples, as part of case studies, is necessary to assess theories related to hormonal influence, discussed above (§2), and to assess stress related to infant-death, considered below. Detailed quantitative coding of case studies will be most valuable and informative in the context of longitudinal population-level data.

(b) Stress

Do nonhuman primate mothers experience stress when their infant dies? Researchers have studied stress in surviving group-mates following adult [40,41] but not infant death. Female baboons showed increases in glucocorticoid stress hormones after adult kin died. Anecdotal cases provide evidence that mothers do experience stress, but we lack quantitative data. For example, a barbary macaque in a tree above her infant-corpse displayed extended bouts of self-grooming and distress calls [32]. How does the death of an infant and carrying affect the mother's social behaviour and social integration? Japanese macaque mothers with dead infants reportedly showed decreased social grooming [22] though this was not quantified. Might this be linked to behaviour indicative of 'depression', with potential for comparison with humans?

For human mothers whose neonate is stillborn, contact, looking at and holding the dead baby, and treating it as a live baby, spending time with, dressing and bathing it, creating memories over the time-limited period available, can benefit psychological well-being [42]. Dead-infant carrying appears phylogenetically ancient. Might carriage and caretaking of the infant-corpse mitigate stress in nonhuman mothers? If so, benefit to fitness may outweigh energetic cost of carrying, at least for short-durations.

Furthermore, it may be asked whether stress increases for bereaved mothers if the infant corpse is removed while she remains motivated to carry it. In captivity, standard procedure is to remove corpses at the first opportunity [21]. Reasons for this include: performing a necropsy while feasible [7], concerns about public perception, lack of knowledge about dead infant-carrying behaviour, or misinterpretation as an abnormal response. Indeed, authors have suggested that early removal might stress mothers [7]. Even with a

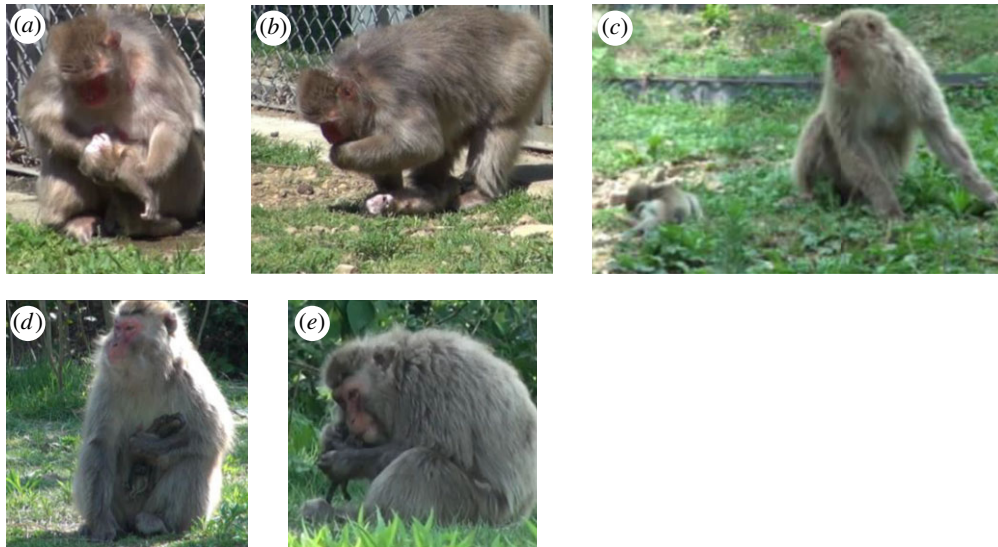


Figure 1. Behavioural responses to infant death: an adult female Japanese macaque holds and inspects her dead infant (a) and lays the infant-corpse on the ground while she forages (b); another female with gaze oriented toward her dead infant (c); a third adult female [8,9] holds/carries the mummified body of her infant 15 days after death (d) and cannibalizes it on day 23 (e). Photo credits: Claire FI Watson. All individuals were captive, socially housed, in large vegetated enclosures (approx. 1400 m²). (Online version in colour.)

Table 3. Behavioural variables to code quantitatively in case reports of mothers with dead infants.

category	focal	behavioural variable
proximity	mother	distance to infant-corpse [3,8,9,16] (interval sampling e.g. every second) approach/retreat to corpse [8,9] (freq.) move between corpse and social group/troop [16] (freq.)
mode of carry	mother	arms/hand, mouth [8,9] (dichotomous)
gaze orientation	mother	head oriented towards/away from corpse [3] (dichotomous)
ad libitum behaviours:	mother; conspecifics	'inspection': peer, touch with hand, inspect [3,8,9] (body; face; anal region); sniff, lick (not anogenital)[8,9]
— infant-directed behaviours		% inspect corpse events followed by hand-sniff [3] 'nurturant': groom [8,9,14]; play [8,9]; lick anogenital region, hold to teats 'protective/defensive': swat fly [3,8]; prevent/block others' interaction with corpse (chase/attack)[8,9]; allow/prevent submersion in water [8,9] cannibalize: eat flesh/dried flesh [8,9]; other: suck/draw past lips [8,9]
— other-directed behaviours	mother	social groom [8,9], number of grooming partners; copulation (while carrying infant-corpse), compare social behaviour and degree of social integration before and after: infant death and carrying period
	mother	species-appropriate behavioural stress indicators: self-groom; self-scratch
	mother	calls [16]; call types
— self-directed behaviours		
— vocalizations		

progressive policy of deferring corpse-removal until mothers lose motivation to carry, judgement can be problematic with appearances potentially misleading without extended observation. Large distances between mother and corpse at any one time may simply represent a repeated approach/retreat pattern. For example, after 22 days of carrying, a macaque mother moved up to 20 m, from her infant-corpse, yet always returned [8,9]. Staff perceived disinterest and removed the corpse. However, when it was

returned to the enclosure 10 minutes later, the mother ran towards it immediately and retrieved it, while threatening nearby humans. This case also underscores the benefit quantitative coding can provide.

Going beyond captivity, we suggest that issues surrounding early removal extend to the field and other taxa, with implications for best practice in husbandry and field policy as well as scientific accuracy and validity. For example, nature-reserve staff retrieved a snub-nosed monkey infant

body for burial when, on the fourth day of carrying, the mother climbed a tree, leaving it below. The mother began vocalizing within half a minute, and continued to search for the corpse all afternoon [14]. A decomposed infant-corpse being pushed along by an adult dolphin was removed by biologists and towed, by boat, to shore for burial. The presumed mother followed, circling and touching the corpse, and remained in shallower waters long after the body was removed [17]. These anecdotal reports together suggest early removal does stress mothers, evidencing strong motivation to continue carrying (but see [15]). Motivation-based approaches to welfare indicate that being prevented from performing behaviours animals are intensely motivated to perform is stressful [43].

If mothers are stressed when their infant dies, does carrying mitigate this stress? Does early removal of the corpse cause stress, and if so, what implications does this have for captive management and field policy? How does the death of her infant in itself, and carrying, affect a mother's social behaviour? To answer all these questions objectively, we need quantitative data on both physiological and behavioural measures before and after infant death and before, during [31] and after infant-corpse carrying. This includes species-appropriate behavioural indicators of negative welfare and stress, for example, increased self-directed behaviours and distress-related vocalization rates. Measures of mothers' social behaviour, for example, social grooming rates and social integration are likely to prove valuable and such data may also allow for better comparisons to behavioural reactions by humans, for example, depressive symptoms of grief including changes in activity patterns and social withdrawal. Because infant death and infant-corpse carrying are unpredictable events, scientists focused on observing this behaviour are unlikely to have taken the relevant pre-mortem measurements in advance. Such important baseline measurements may then necessarily depend on data and hormonal samples gathered for unrelated research and recorded by researchers investigating non-thanatology topics.

5. Conclusion

Understanding nonhuman primate responses to dead infants can contribute to elucidating the evolutionary origins of

human responses to death. However, to fully understand phylogeny, a truly comparative approach will be needed; gathering data from wide-ranging taxa will be key [19], along with interdisciplinary discussion and collaboration. We expect that evidence of inspection and other behavioural responses to dead infants will be found for a wide range of species. Within nonhuman primates alone, current estimates [17] of the number of species displaying infant-corpse carrying and care are probably conservative because many instances go unreported (e.g. wild *Mandrillus sphinx*: M Charpentier 2017, personal communication).

Although documented across many species, mothers' behavioural responses to their dead offspring: dead-infant carrying, inspection, proximity, maternal care such as grooming, protective behaviours and filial cannibalism, remain poorly understood in all. Despite the plethora of proposed explanations, we still lack objective, quantitative data to test each one empirically. Quantitative coding of behavioural responses in individual cases combined with analyses based on appropriate longitudinal records will allow objective evaluation. Potential foci for future observations of death responses are summarized in tables 2 and 3. We seek to encourage and facilitate comparative, quantitative approaches to researching behavioural responses of mothers to their dead infants and have provided a framework to inform future work. Asking the right questions and accumulating relevant observational data will be critical for a more comprehensive understanding of nonhuman responses to death in infants.

Data accessibility. This article has no additional data.

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