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DIGEST

An Individual-Level and Controlled Methodological Framework in Primate Thanatology

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ABSTRACT

How primates sense, cognize, and respond to death, and are affected by it, are broad research themes within primate thanatology. When primate thanatology adopts a comparative framework, it can illuminate the diversity and evolutionary continuity of psycho-neuro-emotional responses to death and dying across primate species, including humans. Evolutionary or comparative thanatology has recently gained momentum, but it lacks methodological consistency, quantitative rigor, and coherent reporting standards. We attempt to address the lack of standardized approaches by introducing an individual-level comparative framework and employing standard ethological methods, accompanied by well-defined behavioral variables. We argue that the proposed framework can capture individual-specific responses to conspecific death and enable hypothesis-driven studies. The framework is essential to examine the large number of hypotheses that have accumulated in the field.

1 | What Is Comparative Thanatology?

Birth and death are coupled phenomena, yet in popular discourses, although birth is largely demystified, death is not. In a theoretical sense, regardless of whether one adopts a physiological [1], psychological [2], or philosophical [3] perspective, discrepancies and debates are a norm in thanatology, that is, the study of death and dying. When combined with potential anthropocentrism and the anthropodenial of sophisticated psychoemotional systems, existing inadequacies in death conceptualizations are magnified in our understanding of primate thanatology [4]. The interrelated disciplines of 'comparative thanatology' and 'evolutionary thanatology' offer a potential resolution, exploring probable continuities in thanatological behavior across humans and nonhumans, including recognition and perception of, and reactions to, the dead and dying. Monsó and Osuna-Mascaró [4] have even argued that developing a concept of death requires 'relatively little cognitive complexity' and is therefore widespread, though graded across species with non-stereotypic responses to death. In contrast, De Marco et al. [5] denounce this proposition and argue that the concept of dormancy as opposed to death is more parsimonious.

Reports surrounding animal deaths from diverse taxa have grown in the scientific literature over the past century, though with caveats such as privileging 'sensationalist' and 'dramatic' thanatological behaviors [5]. Nonetheless, the philosophical and methodological formulations of comparative thanatology are still being developed. Given the crossroads at which the discipline stands, we join the authors of previous appeals in advocating for the adoption of quantitative approaches, though not exclusively. Here, we propose a methodological framework for primates that facilitates an individual-level, multi-controlled, quantitative behavioral assessment (with options to integrate physiological, endocrinological, and psychological factors) of individuals before and after the death of a conspecific. Since death perception is predominantly experiential in a given

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species and varies across individuals, an individual-based approach is essential [6], which we explain below.

2 | What Are the Existing Methods in Primate Thanatology?

The methodological approaches and reporting standards in nonhuman thanatology have been collaterally connected with the diverse philosophies that have dominated the field. Historically, when mentioned at all, nonhuman reactions to the dead and dying have spanned the gamut of reporting, from being scribbled in personal journals half a century ago [7], to the recent publication of meta-analytic articles [8, 9]. Until recently, most behavioral descriptions of thanatological responses were only briefly mentioned in a few experimental and observational studies that focused broadly on mother-infant relationships or inter- and intragroup interactions (e.g., infanticide, territorial conflicts). Thereafter, exclusively case studies were published sporadically until about sixteen years ago [10], when quantitative and hypothesis-driven [11, 12] approaches were added. Although case studies are valuable and offer novel insights, they tend to be qualitative in nature and do not lend themselves to hypothesis testing.

Being opportunistic, most observational studies note corpse-directed behaviors and conspecifics near a corpse, but only when they are salient (e.g., dead infant carrying [13]) or human-like (e.g., silent staring at the corpse by group members in a tight circle [14]). In addition, most naturalistic studies span a very short period following death and use arbitrary indicators as markers of endpoints, such as the subject rejoining their social group or re-socializing. Similarly, short-term reports of maternal and conspecific responses to infant death have either described indifference and prompt attenuation of behavioral reactions, such as nursing and protecting the offspring carcass, or extended manifestation of potentially emotional responses, such as distress vocalizations and self-scratching. In general, studies have disproportionately focused on corpse management by interactors, recording their behavior only when in close spatial proximity to the corpse, and temporally only for a short period after death [5]. Discussions regarding target behaviors (other than the salient ones) of interactors (reflective of the effect of conspecific death), the focal interactor(s), and endpoint markers are absent in the thanatological literature. The few quantitative reports have either adopted a descriptive [15] or an inferential [16] statistical approach, mostly centered on dead infant carrying. Even fewer have adopted a standardized behavioral framework that combines information before (pre-mortem) and after an individual's death (post-death) [17–19], and controlled [11, 20] behaviors of corpse interactors. This is not to state that there have not been appeals for greater quantitative rigor and an overall systematization of techniques and methodologies in the discipline. Most relevant to our proposal is the recommendation by Watson and Matsuzawa [21] for a quantitative treatment of thanatological reports and systematic behavioral comparisons at both individual and group levels.

3 | Multiple Controls to Study Individual-Level Behavioral Responses to Death

Similar to humans, thanatological studies in nonhuman primates (primates, from here on) have revealed extraordinary levels of individual variability in the behavioral response to dead and dying conspecifics, especially among mothers of recently deceased offspring (bereaved mothers). Maternal reactions to the death of offspring, even within a species, may include immediate desertion of a corpse to prolonged carriage [12], protection of corpse to filial cannibalism [20] (not mutually exclusive), decline [11] to an elevated rate of feeding [17], and normative social behavior (including spatial position) to social withdrawal and social avoidance [11]. Graded levels of social withdrawal, aggression, and stress were reported in bonnet macaque (*Macaca radiata*) bereaved mothers [17].

To truly capture the prevalent idiosyncrasies in an individual's reactions to the death of a socially affiliated individual, it is critical to contrast post-mortem behaviors with their pre-mortem analogues. Without prior behavioral information on social affiliates, the causal effect of death on individual-level behavior cannot be established. Therefore, *self controls*, that is, individuals who are their own controls and differ only by their experience of an imminent death, have an evident value in informing our understanding of death recognition, death awareness, and potential mourning (with similarities to 'readjustment-depression' in mother-infant separation studies [22]) in primates. However, *self controls* do not comprehensively contextualize and contrast behavior against external influences such as disruptions in social structure, predatory attacks, or resource fluctuations [23]. Consequently, a *matched control* drawn from the same group, that is, a control comparable in all relevant aspects (such as age, sex, rank, parity, sociability, emotional reactivity, and maternal quality [bereaved mothers]) with the focal interactor and having a distant or no relationship (genetically and socially) with the dead, can compensate for the shortcoming. In essence, *self controls* should be used to draw inferences about the change or stability of an interactor's behavior between pre- and post-mortem periods, and *matched controls* drawn from the focal social group should be used to rule out the influence of extrinsic factors. Combining the two controls can further offer insights into intrinsic individual characteristics (such as emotion and personality) that govern responses to conspecific deaths.

4 | Controlled Pre/Post Quantitative Behavioral Framework

Here, we draw on standard behavioral sampling methods [24] in ethology, to propose a basic field protocol for systematizing and quantifying behavioral approaches to primate thanatology. The protocol provides guidance on selecting focal interactors for the study, determining when to initiate the study, estimating the approximate volume of data to be collected, and categorizing relevant behaviors to be observed across pre-mortem, peri-mortem, and post-mortem conditions for the two proposed controls (Table 1). Determining focal interactor(s) after a conspecific's death is dependent on who consistently expresses corpse-directed behaviors (such as visiting, guarding, or investigating the corpse [10]) and requires no prior information about social relationships. However, the identification of focal interactors in the pre-mortem phase can only be determined retrospectively. Therefore, individuals of social or pair-living species being monitored (i.e., during the pre-mortem phase) under an ongoing study can only be suitable as *self controls*.

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TABLE 1 | Basic ethological framework to study the effect of death on a closely-bonded (focal) interactor.

Attributes	Self control			Matched control
	Pre-mortem	Peri-mortem	Post-mortem	
Choice of focal interactor(s)	Socially/genetically-bonded to the moribund individual	Individuals showing corpse-directed behaviors	Individuals showing corpse-directed behaviors	Unrelated and unconnected
Study start point	≥ 4 days before dying (contingent on data volume below)	Appearance of corpse-directed behaviors	Death of moribund individual	Death of moribund individual
Data volume	≥ 4 diel activity cycles before the emergence of dying symptoms	Throughout dying or temporally spaced out	Continuous or temporally spaced out till stress declines	≥ 4 diel activity cycles
Behaviors of interest[a]				
-*Dying/corpse directed*	Not applicable	Spatial proximity, gaze orientation, vigilance, protection, assistance, food sharing, grooming, transport, resuscitation, etc.	Spatial proximity, protection, care, transport, investigation, aggression, cannibalism, necrophilia, corpse searching/removal, burial, etc.	Not applicable
-*General activities*	Foraging, feeding, passivity, locomotion	Same as pre-mortem	Foraging, feeding, passivity, locomotion	Same as self
-*Stress-related*	Self-directed behaviors (scratching and grooming; 9), yawning, relevant vocalizations, etc.	Self-directed behaviors, yawning, distress vocalizations, etc.	Self-directed behaviors, yawning, silence, distress vocalizations, dead individual-specific calls, etc.	Self-directed behaviors, yawning, distress vocalizations, etc.
-*Spatial position*	Distance from group centroid, #individuals in vicinity [17], relative spatial position, individual/subgroup isolation	Same as pre-mortem	Same as peri-mortem	Distance from group centroid, #members in vicinity, relative spatial position
-*Social behaviors involving group members other than moribund individual*	#Aff approaches initiated, outcome of initiated approaches (S/F), #Aff approaches received, outcome of received approaches (S/F) [11, 21]	Same as pre-mortem	Same as peri-mortem	Same as self
-*Sleep quality*	Change in sleeping posture [25]	Same as pre-mortem	Same as peri-mortem	Same as self

Abbreviations: Aff, Affiliative; F, Failure; S,Success.
[a]Generic behaviors of interest are described, but suitable species-specific behavior should be integrated.

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Implementing a controlled thanatological methodology can be broadened beyond long-term studies if the peri-mortem phase is instead considered as *self controls*, assuming symptoms of imminent fatality are promptly detected and the peri-mortem period is long enough for recording adequate behavioral data.

In contrast, *matched controls* are critically contingent upon the selection of individuals who resemble the focal interactor(s) in as many ways as possible, including their socioecological experiences, and differ only in their recent exposure to death. Consequently, individual(s) for *matched controls* should be chosen from the same social group or a comparable group/pair bond in the same habitat, with the priority being the former. Another crucial element in the framework is the data volume, as determined by the sampling frequency, which should generate sufficient data for robust statistical comparisons. Based on a combination of statistical considerations (such as repeatability and linear regression-based time series analysis) and mother-infant separation studies, we recommend a minimum sampling frequency of four [26, 27] activity cycles (period of activity of an animal in 24 h) in the pre-mortem phase [28], the entire duration of the peri-mortem phase or a minimum of four activity cycles, and finally, four successive activity cycles to study short-term impacts [29]. Since the long-term effects of maternal bereavement may last till the subsequent reproductive phase [16], and the onset is species-specific, it is challenging to determine a minimum sampling frequency for studying long-term effects. Lastly, the framework outlines behaviors that are either corpse-directed or impacted by the death of a conspecific, such as general activities, or are stress indicators. Detailed characterization, measurement, and interpretations of the focal behaviors can be found in the primate thanatology literature. As thanatological reporting expands to different primates, social structures, and physical environments (including captivity), covering broader contexts of death, we foresee a proportionate rise in the diversity of responses death induces and the catalog of species-specific focal behaviors. Even interspecific thanatological observations can be studied within this framework.

Correspondingly, we also anticipate challenges in controlling the effects of intervening factors, which may be ecological, cultural, or social, on species-specific behavioral responses to death. For example, Carter and Huchard [23] highlighted the influence of infants on mothers' social attractiveness in primates. They reasoned that the observed reduction in grooming received, the decline in social companions, and the spatially peripheral positions of bonnet macaque mothers after the death of their infants might not be attributed to infant death, as Arlet et al. [17] reported, but a reduction in their social appeal. This criticism is valid and provides a good example of the importance of selecting appropriate comparisons. In this case, distinguishing between the two potential causal factors might be done by determining when observed behavioral changes can be attributed to bereaved mothers or group members. For example, one might record the frequency of approaches by the mother towards group members and their response (stay/leave), as well as the mother's response (stay/leave) when group members approach her. This will help disentangle the mother's role in the observed social outcomes (such as grooming, hugging, number of neighbors, and spatial position) from that of the group members by assessing whether the mother was the initiator or the recipient of the interaction, what her response was, and the result of the interaction [11]. If the bereaved mother thwarts/seeks social contact, she may desire isolation/companionship, and if the group members avoid her, this would suggest that she has lower social desirability.

5 | Conclusion

Our highlighting of the importance of two complementary controls and our proposal of a corresponding quantitative framework within which to study active and passive behavioral responses to death in primates is not intended to be static, but rather expansive, as the discipline moves into newer avenues and integrates tools from endocrinology, physiology, psychology, and neuroscience. We hope our contribution furthers engagements across taxonomic groups and promotes productive discussions toward an improved understanding of the evolution of reactions to death.

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Data Availability Statement

Data availability statement does not apply to this piece as no primary data were generated and information from published studies were exclusively used.

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