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Signals and cues in death recognition: a quantitative review

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Abstract: Chemicals associated with death are utilized by insects and other animals to mediate their responses to dead conspecifics. For the past decades, there has been an influx of publications associated with death and death-related chemicals, culminating in the introduction of Evolutionary Thanatology in 2018, an interdisciplinary field of study focusing on the phenomena of death and dying across animal taxa. Integrated and interdisciplinary research of chemicals involved in death recognition plays an important role in the formation and growth of this exciting new field from biological and evolutionary perspectives. Here, combining evidence-based Preferred Reporting Items for Systematic Reviews and Meta-analysis (PRISMA) with a keyword co-occurrence analysis, a quantitative review of terminology used in studies of chemicals associated with dead conspecifics was carried out. Given that excessive use of newly coined or improvised terminology and overlapping terms within and between research fields may hinder the growth of this emerging field, we suggest limiting the introduction of novel terminology if existing terms can cover new findings among death-related chemicals. Considering that the field of Evolutionary Thanatology is still in its infancy, *death cue* might be a term-of-choice due to the lack of information on the mechanistic, functional, and evolutionary bases of chemicals associated with dead conspecifics. A standardized/streamlined set of terminology not only affords the opportunity for comparative studies across broad taxa to trace the evolutionary histories of death-related chemicals, but also facilitates the development and growth of Evolutionary Thanatology as a whole.

Key words: death chemical; death cue; terminology; evolutionary thanatology

死亡识别化学信号相关术语的标准化

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摘要：对同类的死亡作出响应并非人类独有，昆虫与其他动物也会面对同类死亡作出相近反应。在过去的几十年，大量与死亡相关的文章相继发表，直至2018年，研究人员整合了所有相关研究并提出了一个新的研究领域——进化死亡学，旨在从进化的角度综合研究人类及其他动物的死亡过程与影响。死亡相关化学物质的研究在该领域的形成和发展过程中发挥了重要作用。在进化死亡学这样的跨学科研究领域，往往会出现由于专业术语不统一而阻碍其发展的现象，因此，专业术语的标准化就显得尤为重要。该文将循证系统评价和荟萃分析中的首选报告项目（Preferred Report-

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ing Items for Systematic Reviews and Meta-analysis，PRISMA）与关键词共现联合分析相结合，对已发表文献中死亡相关化学物质的术语进行了整理和量化分析，总结和探讨了相关术语使用中的主要问题，并对未来相关术语的标准化使用提出了建议。结果表明在已存在可用相关术语的情况下，其他术语仍不断被创造和引入；同一领域内不同术语用于描述相同的概念；相同术语用于描述其他领域的不同概念。由于现有术语已足够描述可能出现的死亡相关化学物质，且目前对死亡及其相关化学物质在调控行为方面的机理和进化知之甚少，建议今后的研究尽量避免引入新术语，并使用死亡信号（death cue）作为描述死亡相关化学物质的标准术语。精简统一的标准化术语不仅有利于从进化角度跨物种比较研究死亡现象，还将推动进化死亡学这一新兴综合学科的整体发展。
关键词：死亡相关化学物质；死亡信号；专业术语；进化死亡学

Death is a natural process, and it is inevitable that even solitary animals encounter the corpses of members of their species. Corpses can harbor dangerous pathogens (Cremer et al., 2007), warn of active competition or predation in the area (Iglesias et al., 2012; Sun & Zhou, 2013), or in some cases, act as a food resource (Sun et al., 2018; Mastrantonio et al., 2021). Therefore, it is important that animals be able to recognize and respond appropriately to conspecific corpses. Animals rely on two general types of information to process their surroundings: signals and cues. Signals are generally defined as stimuli produced by a sender that have evolved to alter the behavior of receivers, while cues also contain information regarding conditions surrounding receivers but have not evolved to specifically alter their behavior (Bradbury & Vehrencamp, 1998; Maynard-Smith & Harper, 2003). For example, volatiles produced by plants after being attacked by herbivores attract parasitoids that defend the plants against herbivores. Through this plant-herbivore-parasitoid co-evolution, volatile compounds that are not essential for plant growth but induced by interactions between the plant host and herbivores can be considered as signals (de Moraes et al., 1998; Price et al., 2011). Inversely, CO_2 is utilized by mosquitoes to locate blood-feeding hosts. CO_2's role in host tracking is completely unintended to the host, who would generally prefer not to be bitten. Therefore, in this case, CO_2 acts as a cue rather than as a signal (Gillies, 1980). In general, it is not easy to assign a chemical compound to a discrete category, as clarification may require a better understanding of the role of the chemical in this sender-receiver interaction (Saleh et al., 2007; Schulte et al., 2015; Garcia et al., 2018). In the case of death recognition, perception of chemicals associated with death can inform animals of the presence of conspecific death, although whether these chemicals exist as signals or as cues are still unclear.

Chemicals emitted when animals die are usually considered reliable and unambiguous (Gonçalves & Biro, 2018; Sun et al., 2018). Among invertebrates, fatty acids play a role in mediating general corpse avoidance behaviors (Yao et al., 2009) as well as social insect-specific behaviors such as burial, cannibalism and corpse removal (Wilson et al., 1958; Sun et al., 2017; McAfee et al., 2018). Among vertebrates, cadaverine and putrescine, two chemicals associated with putrefaction, are found to typically induce an aversive response (Carr et al., 1981; Pinel et al., 1981; Anderson et al., 2021). Novel chemicals continue to be identified that are utilized by non-human animals in moderating their responses to death, mostly in social insects (co-opted pheromones in honeybee, vanishing life signs in ants, early death cues in termites) (Sun et al., 2018). Moreover, chemicals associated with death are found not only as simple substances but also as finely proportioned blends in the honeybee *Apis cerana* (Klett et al., 2021) and termite *Pseudacanthotermes spiniger* (Chouvenc et al., 2012). Researchers use a variety of terms to describe these chemicals, including both *death cue* (Choe et al., 2009; Sun & Zhou, 2013; Qiu et al., 2015) and *death signal* (Howard & Tschinkel, 1976; Rollo et al., 1995; Latanville & Stone, 2013), in addition to terms such as *funeral pheromone* (Ali & Morgan, 1990; Bomar & Lockwood, 1994), *death pheromone* (Deming, 2005; Engel, 1991), and *necromone* (Rollo et al., 1994; Yao et al., 2009). Given the array of terminology used to describe the chemicals involved in death recognition, it is worth questioning what is gained by the use of so many different terms and whether the field would benefit from streamlining this terminology.

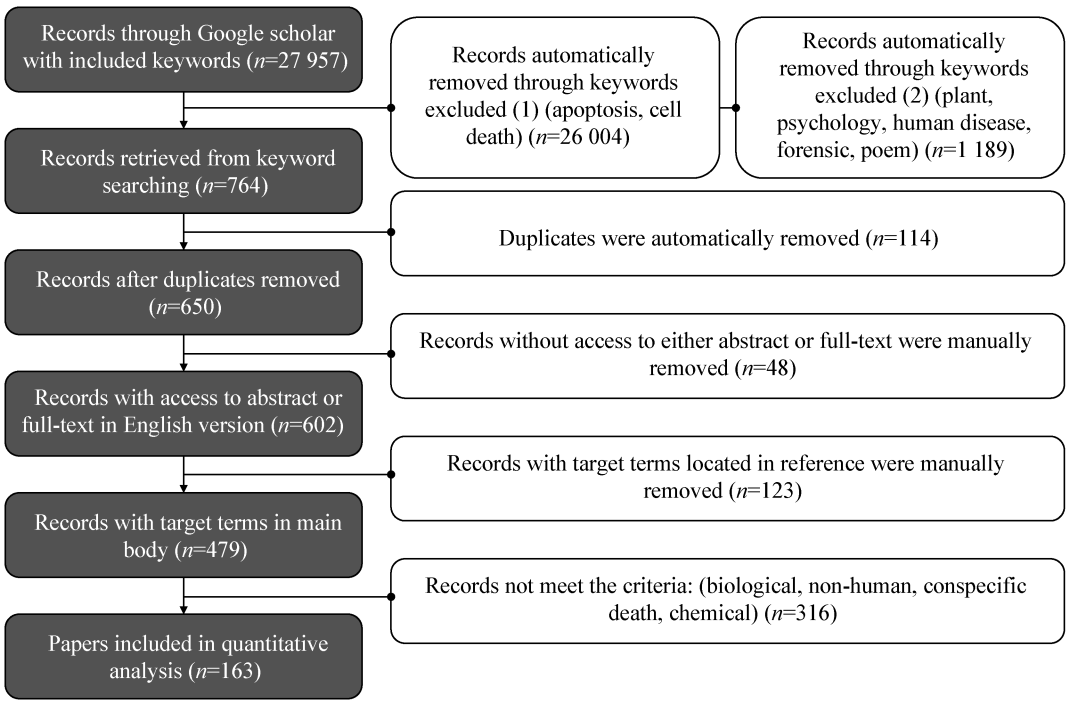
Streamlining terminology can help to avoid unnecessary confusion and develop precise communication for research integration in an already complicated field (Stock & Burton, 2011; Peacor et al., 2020). As a fundamental component of the overarching field of Evolutionary Thanatology, research on the chemicals involved in death recognition across taxa represents the first step towards understanding death from a biological perspective. Evolutionary Thanatology is an emerging field of integrated studies examining the phenomena of death and dying (Anderson et al., 2018), focusing on the proximate and ultimate explanations of how living organisms deal with the deaths of conspecifics from both biological and sociological standpoints. From a sociological aspect, interest exists in topics related to the cognitive understanding of death (Anderson, 2018; Longbottom & Slaughter, 2018) and the influence of death on human behavior and culture (Humphrey, 2018; Husband, 2018; Shimane, 2018). Biological research under Evolutionary Thanatology focuses on the underlying mechanisms and evolutionary significance of death recognition, as well as behavioral responses to the dead, and broadens the research horizon from only human beings to the entire animal kingdom, including arthropods (Yao et al., 2009; Sun & Zhou, 2013), crustaceans (Small & Thacker, 1994; Candia-Zulbarán et al., 2015), amphibians and reptiles (Babbitt & Meshaka, 2000; Siqueira et al., 2015), fish (Oliveira et al., 2014; Stroud et al., 2014), birds (Iglesias et al., 2012; Swift & Marzluff, 2015; 2018), and aquatic and terrestrial mammals (McComb et al., 2006; Prounis & Shields, 2013). This integrated field covers topics from insects' responses to chemicals emitted by their dead conspecifics to the human understanding of death and provides opportunities to explore the biological basis and evolution of death-related behavioral traits and psychological activities. Death-related chemicals across all biological taxa are already complicated and applying terminology without clear reasoning could potentially obstruct the integration of research in this area.

Clarifying terminology improves accuracy and efficiency of communication while reducing possible uncertainty and confusion. Given these benefits, is it possible to summarize the terminology used in death recognition and streamline it into simple definitions and terms? In this review, a quantitative literature review following evidence-based Preferred Reporting Items for Systematic Reviews and Meta-analysis (PRISMA) guidelines with a keyword co-occurrence analysis and a summary of terminology used in studies of death recognition was carried out. The primary issues of such terminology were discussed, and suggestions were given regarding how to streamline terminology for future publications.

1 Materials and Methods

1.1 Collection and screening of papers

A restricted literature search was conducted on December 2021 to identify studies of death recognition in non-human animals, following PRISMA guidelines (Moher et al., 2009). The literature was searched in Google Scholar (https://scholar.google.com), using a subset of related keywords (*dead conspecific*, *necromone*, *funeral pheromone*, *corpse cue*, *corpse signal*, *corpse pheromone*, *cadaver cue*, *cadaver signal*, *cadaver pheromone*, *death recognition signal*, *death recognition cue*, *death recognition pheromone*, *death cue*, *death signal*, *death pheromone*, *necrophobic cue*, *necrophobic signal*, *necrophobic pheromone*, *necrophoric cue*, *necrophoric signal*, *necrophoric pheromone*). Papers were selected if they met the following criteria: 1) the term was used with reference to non-human animals; 2) the study was conducted on the organismal level (studies at the cellular level were excluded, i.e. apoptosis); 3) the term included chemicals associated with dead conspecifics; 4) the topic focused on a biological area; and 5) an English version of the abstract or full-text was available. Duplicate papers were removed manually. A flowchart of the search and selection process is presented in Fig. 1. Text information of titles and abstracts was retrieved from the Web of Science Core Database for content analysis. Terms associated with dead conspecifics were manually located in the main bodies of each paper and extracted for summarization.



The number of records included or excluded in each step is shown.

Fig. 1 Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA) flowchart for paper selection

1.2 Searching for commonly used terms using co-occurrence analysis

A term co-occurrence map was constructed based on terms extracted from titles and abstracts using binary counting (only presence of the terms mattered, the number of occurrences of a term in a paper was not taken into account) in the software VOSviewer 1.6.17 (Leiden University, Leiden, Netherlands). A total of 3 135 terms were retrieved; the minimum number of occurrences of a term for it to be used in our analysis was set as three, with 202 terms meeting this threshold. Of the 202 terms, general abstract terms like *hypothesis*, *research*, *researcher*, and *study* were excluded. Similar terms were combined, for example, *Reticulitermes flavipes*, *R. flavipes*, *termites*, and *subterranean termites* were all replaced by *termite*, while *odorant*, *odour*, *scent*, and *smell* were all replaced by the term *odor*. In the end, 97 terms were included for visualization of term occurrence.

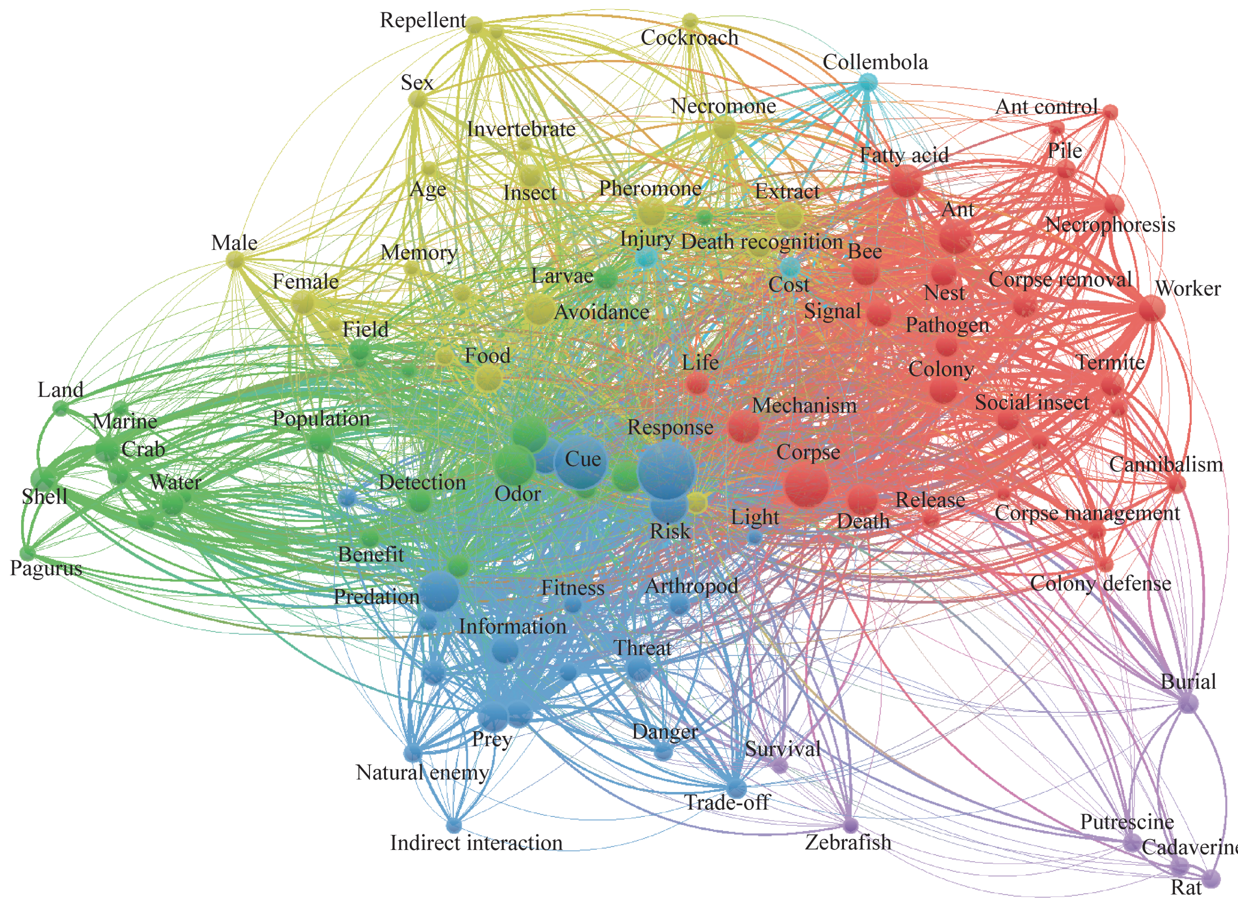
1.3 Visualizing relationships among commonly used terms using a Venn diagram

Based on the data derived from the co-occurrence analysis, terms used to describe death-related chemicals were categorized into five types: *cue*, *signal*, *pheromone*, *necromone*, and *others*. Terms with multiple target phrases, such as "a necromone cue" (Shephard et al., 2018), were assigned to both relevant categories, i.e., *necromone* and *cue*. The occurrence of each type of term was binarily counted and summarized as decade trends. Overlapping among the five types was illustrated and compared in a Venn diagram (http://eulerr.co).

2 Results

2.1 Commonly used terms in death-related chemicals

A co-occurrence analysis was performed on the titles and abstracts of papers selected through a restricted literature search to identify commonly used terms among death-related chemicals. Of the 97 terms included for occurrence visualization, 14 were generally used in relation to chemicals: *cue*, *odor*, *chemical*, *fatty acid*, *information*, *pheromone*, *extract*, *signal*, *necromone*, *cadaverine*, *putrescine*, *volatile*, *chemical signature*, and *chemical stimuli*. *Fatty acid*, *cadaverine*, and *putrescine* directly refer to specific chemicals. *Odor*, *chemical*, *information*, *extract*, *volatile*, *chemical signature*, and *chemical stimuli* are non-specific references to chemical substances. *Cue*, *pheromone*, *signal*, and *necromone* indicate such chemicals play a role in death recognition. A mapping network was constructed to graphically visualize the co-occurrence relationships between these terms (Fig. 2). Each node represents a term, and the size of a node is proportional to the occurrence of its term. Links between terms indicate co-occurrence. Terms are positioned according to relatedness, such that the closer together two terms are, the more often they co-occurred in our analysis.



Nodes represent keywords (*n*=27). Sizes of nodes indicate occurrence of each keyword. Links between nodes indicate that both references occurred in same paper. Different colors of nodes indicate different clusters representing different topics (*n*=6).

Fig. 2 Network mapping of co-occurrence of keywords extracted from titles and abstracts of selected papers

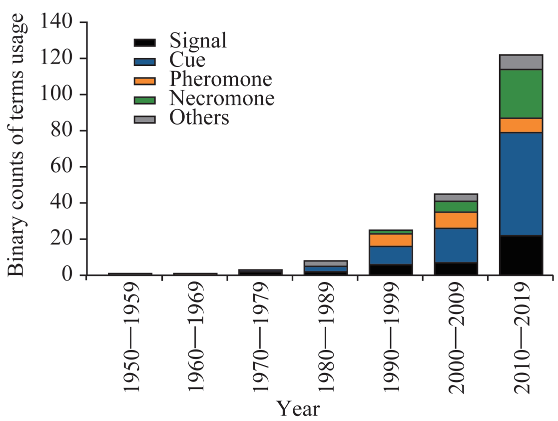
Furthermore, terms were grouped into six clusters based on their overall relatedness to each other. Cluster 1 (red) is the largest and contains 26 terms, including terms such as *chemical signature*, *fatty acid*, and *signal*. Cluster 2 (green) contains 22 terms and includes terms such as *chemical*, *chemical stimuli*, and *odor*. Cluster 3 (blue) contains 20 terms and includes terms such as *cue* and *information*. Cluster 4 (yellow) contains 20 terms, including *extract*, *necromone*, *pheromone*, and *volatile*. Cluster 5 (purple) and 6 (cyan) are the two smallest clusters with six (including *cadaverine* and *putrescine*) and three terms (*Collembola*, *cost*, and *injury*), respectively (Table 1).

2.2 Relationships among commonly used terms

Among the retained papers (*n*=163), 219 binary counts of terms associated with death-related chemicals were collected and assigned into one or more of five categories: *cue*, *signal*, *pheromone*, *necromone*, and *others*. Terms with low occurrence such as *the odor of dead conspecifics* (Tricarico et al., 2011), *necrophoric behavior releaser* (Tricarico et al., 2011), *death recognition chemical* (Sun & Zhou, 2013), and *conspecific alarm* (Latanville & Stone, 2013) were assigned to *others*. Time trends of terms used from 1950 to 2019 were summarized by decade in Fig. 3. Usage of terms associated with death-related chemicals has increased in each decade since the 1950s. Incidence of term usage since 2000 is almost fivefold that of all pre-2000 papers. Among terms, *cue* appeared most often (n=93, 42.5%), followed by *signal* (n=43, 19.6%) and *necromone* (n=40, 18.3%). *Pheromone* was used in 27 papers (12.3%), while terms in *others* were used in 16 papers (7.3%) (Fig. 3). Binary counts of terms from papers since 2020 are not illustrated in Fig. 3 given that only two years' worth of publications is available.

Table 1 Summary of commonly used terms in death-related chemicals based on co-occurrence analysis

Cluster	Color	No. of terms	Term (occurrence)	Main topics
1	Red	26	Fatty acid (18), signal (12), chemical signature (3)	Mechanism of corpse management in social insects
2	Green	22	Odor (30), chemical (22), chemical stimuli (3)	Using death-related chemicals in aquatic crustaceans
3	Blue	20	Cue (57), information (13)	Death cue of conspecifics as indirect cue in risk assessment of predation
4	Yellow	20	Pheromone (13), extract (12), necromone (8), volatile (4)	Extract of dead conspecifics eliciting avoidance in insects and could be used as repellency
5	Purple	6	Cadaverine (4), putrescine (4)	Cadaverine and putrescine elicit burial behavior in rats
6	Cyan	3	Not applicable	Not applicable



Stacked histogram depicting the five main terms used for death-related chemicals summarized by incidence per decade from 1950 to 2019. Different colors indicate different terms.

Fig. 3 Decade trends in terminology in death-related chemical research

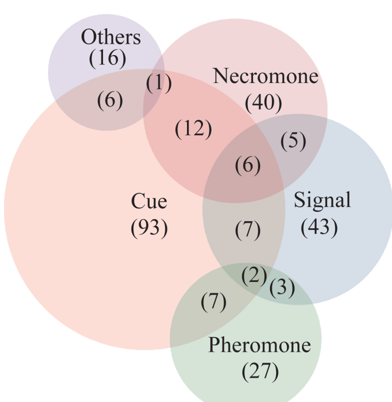
A Venn diagram demonstrating the relationship between each type of term is shown in Fig. 4. *Cue* overlapped with all four other term types. Nineteen papers used *cue* along with *necromone*, 15 used it with *signal*, nine with *pheromone*, and six with *others*. Moreover, five papers used both *signal* and *pheromone*, and 11 papers used both *signal* and *necromone*. A total of 43 (26.4%) papers used more than one type of term for chemicals associated with dead conspecifics.

3 Discussion

A quantitative literature review to identify major terms associated with death-related chemicals and to delineate the relationships among them was performed. Other than the names of chemicals and nonspecific terms such as *odor*, *chemical*, and *chemical stimuli,* four terms were extensively used to describe chemicals involved in death recognition: *signal*, *cue*, *pheromone*, and *necromone*. Furthermore, clustering analysis showed clear trends in research topics and term usage among and within clusters (Fig. 2, Table 1). In eusocial insects, *signal*, *fatty acid*, and *chemical signature* were terms commonly associated with corpse management, whereas *pheromone*, *necromone*, *extract,* and *volatile* were commonly associated with necrophobic responses to chemicals emitted by dead conspecifics. In aquatic crustaceans, *odor*, *chemical*, and *chemical stimuli* were commonly used terms. *Cadaverine* and *putrescine* were commonly mentioned by exact chemical name when referring to the burial behavior of rats. *Cue* and *information* were commonly used in cases where dead conspecifics were considered as indirect information in assessing the risk of predation. In the following sections, some of the issues associated with the usage of terminology in the study of death-related chemicals were summarized.

3.1 Some newly coined terms might be inconsistent with existing/established terminology

Since E. O. Wilson and his colleagues' pioneering discovery of fatty acids eliciting corpse removal behavior in ants (Wilson et al., 1958), interest in death-related chemicals has rapidly increased, leading to the introduction of a host of terms used to refer to these chemicals (Fig. 2). The work to streamline the terminology in this area began in 1994 when Rollo et al. (1994) introduced the term *necromone* to describe the common insect death-related chemicals, fatty acids. Prior to the introduction of *necromone*, for example, fatty acids had been referred to as *pheromones* in relation to ant corpse removal behavior in 1963 (Wilson, 1963), *necrophoric signal*s in 1976 (Howard & Tschinkel, 1976), 1983 (Visscher, 1983) and 1985 (Sorensen et al., 1985), *funeral pheromone*s in 1990 (Ali & Morgan, 1990) and *death pheromones* in 1991 (Engel, 1991). However, *necromone* failed to become a dominant term within the field and was followed by multiple newly coined terms, such as *corpse recognition signal* (Akino & Yamaoka, 1996), *death-recognition signal* (Nilsson & Bengtsson, 2004), *necrophoric pheromone* (Gordon, 2010). Such inconsistency might lead to confusion in terminology, especially for interdisciplinary research (Neal & Anderson, 2005; Chamberlain-Salaun et al., 2013).



Relationships among usage of death-related chemical terms. Numbers in parentheses indicate binary counts of each term in selected papers. Numbers in overlapping regions indicate the number of papers in which two or more terms appeared together. The area of each shape is proportional to the number of elements it contains.

Fig. 4 Relationships among the five main death-related chemical terms

While discoveries of novel death-related chemicals continue to be made, these discoveries do not necessarily lead to the introduction of new terminology. The disappearance of two chemical *signals* associated with life, dolichodial and iridomyrmecin, after death was found in 2009 to reveal the fatty acid *death cue*, oleic acid, and trigger corpse removal in ants (Choe et al., 2009). Two volatiles, 3-octanol and 3-octanone, were identified as early *death cues* in the termite *R. flavipes* in 2017 that are released immediately after death and recruit workers to cannibalize the dead conspecific (Sun et al., 2017). *β*-ocimene, a brood *pheromone* involved in food begging by honeybee brood, was identified in 2018 as being released by brood after death and together with oleic acid, the *death cue*, induced brood removal behavior by workers (McAfee et al., 2018). In each case, existing terms for death-related chemicals were used following these discoveries, indicating a pool of commonly accepted terms within the literature. If the existing/established pool of terminology can cover the new discoveries, there is no need to reinvent the wheel.

3.2 Overlapping terms can lead to confusion in terminology

"Overlapping terms" refers to either multiple terms describing the same concept or a single term representing different concepts. Specifically, as shown in Fig.4, overlaps indicate cases where different terms are used to refer to the same death-related chemicals within a single paper. For example, both *cue* and *necromone* were used to refer to oleic acid released during decomposition in termites (Ulyshen & Shelton, 2012); *cue*, *signal*, and *necromone* were all used to describe chemicals released by dead (Rollo et al., 1995); and *necromone* and *death pheromone* were used to refer to fatty acids in the honeybee (Kathe et al., 2021), as well as *cue* and *death pheromone* (Dukas, 1998). These overlaps can also be explained by combinations of existing terms into one. For example, *necromone cues* (Yao et al., 2009; Shephard et al., 2018; Gervais & Brown, 2021) and *necromone signals* (Yao et al., 2009; Aksenov & David Rollo, 2017). Both of these two use cases may reflect blurry boundaries of concepts and ambiguity in term selection. Moreover, some terms used to refer to death-related chemicals are commonly used in other fields. Although it is used to refer to chemicals released by dead animals (Howard & Tschinkel, 1976; Rollo et al., 1995; Latanville &

Stone, 2013), *death signal* also refers to chemicals signaling cell death (i. e. apoptosis) (Elmore, 2007). A search in Google Scholar using the keyword *death signal* would yield over 26 200 papers as of December 2021, of which the majority (more than 95%) are related to apoptosis rather than death-related chemicals on an organismal level. Overlap of terminology with other fields further obfuscates the ability of those studying death-related chemicals to locate publications on the topic.

3.3 Signal or cue?

Our analysis revealed that *cue* is a dominant term used among death-related chemicals (Fig. 4). Of the remaining major terms, *pheromone* refers to signals between animals of the same species (Karlson & Lüscher, 1959), while the term *necromone* is created by combining the words *necro-* and *pheromone* but is not necessarily constrained to chemicals that would be considered pheromones and as a result is too vague to be distinct from other terms (Rollo et al., 1994). Overall, *signal* (including both *signal* and *pheromone*) and *cue* are the two main terms used for chemicals involved in death recognition. Based on the definition, death-related chemicals could be considered as signals only if their role as such has feasibly been shaped by natural selection to alter another animal's behavioral responses to the dead, otherwise they should be classified as cues (Greenfield, 2002). However, the underlying role and evolution of some chemicals related to death recognition remains unclear. For example, in the case of 3-octanol and 3-octanone released immediately after death in the termite *R. flavipes*, it is suggested to help living termite workers locate freshly dead nestmates (Sun et al., 2017). It is better to classify them as cues since it is still unknown if any specialized features could indicate that these two volatiles have evolved to shorten the time required to initiate corpse management and facilitate the fitness of the colony.

The dominance of *cue* as a term suggests that the nature of these death-related chemicals is far from resolved. The attempt to distinguish these two concepts would help guide investigations into the roles and evolution of specific chemicals in death recognition. Across taxa, chemicals utilized by animals in death recognition range from single chemicals such as fatty acids, cadaverine, and putrescine that elicit avoidance responses (Yao et al., 2009; Anderson et al., 2021) to complex blends or co-operation between chemicals in eusocial insects that induce burial or corpse removal behaviors (Chouvenc et al., 2012; McAfee et al., 2018; Klett et al., 2021). Without evidence indicating the existence of evolution among these chemicals, these chemicals cannot be defined as signals. Studies of death-related chemicals are still in their infancy and basic knowledge concerning the mechanisms and evolution of these chemicals, in large part, remains unclear. In the current stage of the field, we suggest using *death cue* in reference to death-related chemicals as a more conservative solution.

4 Summary and perspectives

In this quantitative review of terminology associated with chemicals related to conspecific death, we have discussed current issues related to the use of both newly coined terminology and overlapping terms within and between research fields, and how these issues may unintentionally impede the development of the emerging integrated field of Evolutionary Thanatology. Considering that our current terminology should suffice for existing and future discoveries in death-related chemicals, we recommend restricting the introduction of new terms in future publications. As research in Evolutionary Thanatology is still at the beginning stage of its development, we suggest the use of *death cue* for death-related chemicals rather than *signal* unless the evolution of a chemical specifically for death recognition is confirmed. As the field of Evolutionary Thanatology continues to grow, a standardized and streamlined terminology will allow us to carry out comparative studies across different taxa to trace the potential evolutionary history of death-related chemicals and behavioral responses.

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References

Akino T, Yamaoka R. 1996. Origin of oleic acid, corpse recognition signal in the ant, *Formica japonica* Motschlsky (Hymenoptera: Formicidae). Japanese Journal of Applied Entomology and Zoology, 40(4): 265−271

Aksenov V, David Rollo C. 2017. Necromone death cues and risk avoidance by the cricket *Acheta domesticus*: effects of sex and duration of exposure. Journal of Insect Behavior, 30(3): 259−272

Ali MF, Morgan ED. 1990. Chemical communication in insect communities: a guide to insect pheromones with special emphasis on social insects. Biological Reviews, 65(3): 227−247

Anderson JR. 2018. Chimpanzees and death. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 373(1754): 20170257

Anderson JR, Biro D, Pettitt P. 2018. Evolutionary thanatology. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 373(1754): 20170262

Anderson JR, Yeow H, Hirata S. 2021. Putrescine: a chemical cue of death - is aversive to chimpanzees. Behavioural Processes, 193: 104538

Babbitt KJ, Meshaka WE Jr. 2000. Benefits of eating conspecifics: effects of background diet on survival and metamorphosis in the Cuban treefrog (*Osteopilus septentrionalis*). Copeia, 2000(2): 469−474

Bomar CR, Lockwood JA. 1994. Olfactory basis of cannibalism in grasshoppers (Orthoptera: Acrididae) I: laboratory assessment of attractants. Journal of Chemical Ecology, 20(9): 2249−2260

Bradbury JW, Vehrencamp SL. 1998. Principles of animal communication. Sunderland, US: Sinauer Associates, pp. 3−5

Candia-Zulbarán RI, Briones-Fourzán P, Lozano-Álvarez E, Barradas-Ortiz C, Negrete-Soto F. 2015. Caribbean spiny lobsters equally avoid dead and clinically PaV_1-infected conspecifics. ICES Journal of Marine Science, 72(S): 164−169

Carr WJ, Landauer MR, Sonsino R. 1981. Responses by rats to odors from living versus dead conspecifics. Behavioral and Neural Biology, 31(1): 67−72

Chamberlain-Salaun J, Mills J, Usher K. 2013. Terminology used to describe health care teams: an integrative review of the literature. Journal of Multidisciplinary Healthcare, 6: 65−74

Choe DH, Millar JG, Rust MK. 2009. Chemical signals associated with life inhibit necrophoresis in Argentine ants. Proceedings of the National Academy of Sciences of the United States of America, 106(20): 8251−8255

Chouvenc T, Robert A, Sémon E, Bordereau C. 2012. Burial behaviour by dealates of the termite *Pseudacanthotermes spiniger* (Termitidae, Macrotermitinae) induced by chemical signals from termite corpses. Insectes Sociaux, 59(1): 119−125

Cremer S, Armitage SAO, Schmid-Hempel P. 2007. Social immunity. Current Biology, 17(16): R693−R702

de Moraes CM, Lewis WJ, Paré PW, Alborn HT, Tumlinson JH. 1998. Herbivore-infested plants selectively attract parasitoids. Nature, 393(6685): 570−573

Deming AH. 2005. With animals in mind. The Georgia Review, 59(3): 456−470

Dukas R. 1998. Cognitive ecology: the evolutionary ecology of information processing and decision making. Chicago: The University of Chicago Press, pp. 129−174

Elmore S. 2007. Apoptosis: a review of programmed cell death. Toxicologic Pathology, 35(4): 495−516

Engel R. 1991. From molecules to life.//Agazzi E, Cordero A. Philosophy and the origin and evolution of the universe. Dordrecht: Springer, pp. 203−218

Garcia JE, Shrestha M, Howard SR, Petersen P, Dyer AG. 2018. Signal or cue: the role of structural colors in flower pollination. Current Zoology, 65(4): 467−481

Gervais CR, Brown C. 2021. Impact of conspecific necromones on the oxygen uptake rates of a benthic elasmobranch. Animal Behaviour, 174: 1−8

Gillies MT. 1980. The role of carbon dioxide in host-finding by mosquitoes (Diptera: Culicidae): a review. Bulletin of Entomological Research, 70(4): 525−532

Gonçalves A, Biro D. 2018. Comparative thanatology, an integrative approach: exploring sensory/cognitive aspects of death recognition in vertebrates and invertebrates. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 373(1754): 20170263

Gordon DM. 2010. Ant encounters: interaction networks and colony behavior. Princeton: Princeton University Press

Greenfield MD. 2002. Signalers and receivers: mechanisms and evolution of arthropod communication. New York: Oxford University Press

Howard DF, Tschinkel WR. 1976. Aspects of necrophoric behavior in the red imported fire ant, *Solenopsis invicta*. Behaviour, 56(1/2): 157−178

Humphrey N. 2018. The lure of death: suicide and human evolution. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 373(1754): 20170269

Husband EM. 2018. Speaking of death. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 373 (1754): 20180172

Iglesias TL, McElreath R, Patricelli GL. 2012. Western scrub-jay funerals: cacophonous aggregations in response to dead conspecifics. Animal Behaviour, 84(5): 1103−1111

Karlson P, Lüscher M. 1959. ‘Pheromones’: a new term for a class of biologically active substances. Nature, 183(4653): 55−56

Kathe E, Seidelmann K, Lewkowski O, Conte Y, Erler S. 2021. Changes in chemical cues of *Melissococcus plutonius* infected honey bee larvae. Chemoecology, 31(3): 189−200

Klett K, Zhang JJ, Zhang YY, Wang ZW, Dong SH, Tan K. 2021. The Nasonov gland pheromone as a potential source of death cue in *Apis cerana*. Journal of Insect Physiology, 131: 104238

Latanville JK, Stone JR. 2013. Pesticide and predation exposure effects on pond snail immune system function and reproductive output. Journal of Shellfish Research, 32(3): 745−750

Longbottom S, Slaughter V. 2018. Sources of children’s knowledge about death and dying. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 373(1754): 20170267

Mastrantonio V, Crasta G, Urbanelli S, Porretta D. 2021. Cannibalism and necrophagy promote a resource loop and benefit larval development in insects of temporary waters. Insects, 12(7): 657

Maynard-Smith J, Harper D. 2003. Animal signals. Oxford: Oxford University Press, pp. 3−6

McAfee A, Chapman A, Iovinella I, Gallagher-Kurtzke Y, Collins TF, Higo H, Madilao LL, Pelosi P, Foster LJ. 2018. A death pheromone, oleic acid, triggers hygienic behavior in honey bees (*Apis mellifera* L.). Scientific Reports, 8: 5719

McComb K, Baker L, Moss C. 2006. African elephants show high levels of interest in the skulls and Ivory of their own species. Biology Letters, 2(1): 26−28

Moher D, Liberati A, Tetzlaff J, Altman DG, Group PRISAA. 2009. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. Annals of Internal Medicine, 151(4): 264−269

Neal PR, Anderson GJ. 2005. Are ‘mating systems’ ‘breeding systems’ of inconsistent and confusing terminology in plant reproductive biology? or is it the other way around? Plant Systematics and Evolution, 250(3/4): 173−185

Nilsson E, Bengtsson G. 2004. Endogenous free fatty acids repel and attract Collembola. Journal of Chemical Ecology, 30(7): 1431−1443

Oliveira TA, Koakoski G, da Motta AC, Piato AL, Barreto RE, Volpato GL, Barcellos LJG. 2014. Death-associated odors induce stress in zebrafish. Hormones and Behavior, 65(4): 340−344

Peacor SD, Barton BT, Kimbro DL, Sih A, Sheriff MJ. 2020. A framework and standardized terminology to facilitate the study of predation-risk effects. Ecology, 101(12): e03152

Pinel JPJ, Gorzalka BB, Ladak F. 1981. Cadaverine and putrescine initiate the burial of dead conspecifics by rats. Physiology & Behavior, 27(5): 819−824

Price PW, Denno RF, Eubanks MD, Finke DL, Kaplan I. 2011. Insect ecology: behavior, populations and communities. Cambridge: Cambridge University Press

Prounis GS, Shields WM. 2013. Necrophobic behavior in small mammals. Behavioural Processes, 94: 41−44

Qiu HL, Lu LH, Shi QX, Tu CC, Lin T, He YR. 2015. Differential necrophoric behaviour of the ant *Solenopsis invicta* towards fungal-infected corpses of workers and pupae. Bulletin of Entomological Research, 105(5): 607−614

Rollo CD, Borden JH, Casey IB. 1995. Endogenously produced repellent from American cockroach (Blattaria: Blattidae): function in death recognition. Environmental Entomology, 24(1): 116−124

Rollo CD, Czvzewska E, Borden JH. 1994. Fatty acid necromones for cockroaches. Naturwissenschaften, 81(9): 409−410

Saleh N, Scott AG, Bryning GP, Chittka L. 2007. Distinguishing signals and cues: bumblebees use general footprints to generate adaptive behaviour at flowers and nest. Arthropod-Plant Interactions, 1(2): 119−127

Schulte LM, Krauss M, Lötters S, Schulze T, Brack W. 2015. Decoding and discrimination of chemical cues and signals: avoidance of predation and competition during parental care behavior in sympatric poison frogs. PLoS ONE, 10(7): e0129929

Shephard AM, Aksenov V, Rollo CD. 2018. Conspecific mortality cues mediate associative learning in crickets, *Acheta domesticus* (Orthoptera: Gryllidae). Journal of Orthoptera Research, 27(2): 187−192

Shimane K. 2018. Social bonds with the dead: how funerals transformed in the twentieth and twenty-first centuries. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 373(1754): 20170274

Siqueira RMS, Coeti RZ, Cavalheri DG, Trevine V, Almeida-Santos SM. 2015. The sexual attractiveness of the corpse bride: unusual mating behaviour of *Helicops carinicaudus* (Serpentes: Dipsadidae). Herpetology Notes 8, 643−647

Small MP, Thacker RW. 1994. Land hermit crabs use odors of dead conspecifics to locate shells. Journal of Experimental Marine Biology and Ecology, 182(2): 169−182

Sorensen AA, Fletcher DJC, Vinson SB. 1985. Distribution of inhibitory queen pheromone among virgin queens of an ant, *Solenopsis invicta*. Psyche, 92: 071928

Stock P, Burton RJF. 2011. Defining terms for integrated (multi-inter-trans-disciplinary) sustainability research. Sustainability, 3(8): 1090−1113

Stroud EM, O’onnell CP, Rice PH, Snow NH, Barnes BB, Elshaer MR, Hanson JE. 2014. Chemical shark repellent: myth or fact? The effect of a shark necromone on shark feeding behavior. Ocean & Coastal Management, 97: 50−57

Sun Q, Haynes KF, Zhou XG. 2017. Dynamic changes in death cues modulate risks and rewards of corpse management in a social insect. Functional Ecology, 31(3): 697−706

Sun Q, Haynes KF, Zhou XG. 2018. Managing the risks and rewards of death in eusocial insects. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 373 (1754): 20170258

Sun Q, Zhou XG. 2013. Corpse management in social insects. International Journal of Biological Sciences, 9(3): 313−321

Swift KN, Marzluff JM. 2015. Wild American crows gather around their dead to learn about danger. Animal Behaviour, 109: 187−197

Swift K, Marzluff JM. 2018. Occurrence and variability of tactile interactions between wild American crows and dead conspecifics. Philosophical Transactions of the Royal, Society B: Biological Sciences 373(1754): 20170259

Tricarico E, Breithaupt T, Gherardi F. 2011. Interpreting odours in hermit crabs: a comparative study. Estuarine, Coastal and Shelf Science, 91(2): 211−215

Ulyshen MD, Shelton TG. 2012. Evidence of cue synergism in termite corpse response behavior. Naturwissenschaften, 99(2): 89−93

Visscher PK. 1983. The honey bee way of death: necrophoric behaviour in *Apis mellifera* colonies. Animal Behaviour, 31(4): 1070−1076

Wilson EO. 1963. Pheromones. Scientific American, 208(5): 100−114

Wilson EO, Durlach NI, Roth LM. 1958. Chemical releasers of necrophoric behavior in ants. Psyche, 65: 069391

Yao M, Rosenfeld J, Attridge S, Sidhu S, Aksenov V, Rollo CD. 2009. The ancient chemistry of avoiding risks of predation and disease. Evolutionary Biology, 36(3): 267−281

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