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Review Article

Death feigning in ants

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Abstract

In many animals, feigning death is a last resort to avoid being killed by a predator or competitor. While the neurological and physiological correlates of death feigning (DF) as well as its adaptive significance have intensively been studied in numerous arthropods, detailed studies on this phenomenon in ants are rare. Here, we describe DF in ants in detail and show that in many species it can be provoked by experimental manipulation or staged encounters with aggressive competitors in the laboratory. Much less is known about the context and consequence of death feigning in nature and whether it successfully protects ants from ant-eating predators or territorial intruders. We suggest additional research on this often neglected, but easily studied phenomenon, which will help to increase our understanding of its importance and underlying causes.

Key words: Thanatosis, tonic immobility, apparent death, defense, Hymenoptera, Formicidae, review.

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Introduction

Predation and competition are powerful agents of selection and drive the evolution of morphological, physiological, and chemical defenses, such as spines, toxins, mimicry, or camouflage, and also behavioral defenses, such as autotomy, dropping, or rolling away (for reviews, see Humphreys & Ruxton 2018, 2019, Sugiura 2020, Sakai 2021).

One long known behavioral strategy consists of feigning death. It is usually employed as a last alternative when the individual has already been detected and attacked by a predator or competitor. In short, the individual assumes an immobile posture and in several species also emits an unpleasant smell. In this way, it pretends to be an unpalatable corpse, which discourages and / or confuses at least those predators that avoid dead animals (Rogers & Simpson 2014, Humphreys & Ruxton 2018, Carli & Farabollini 2022). The adaptive value and physiological correlates of death feigning have been thoroughly investigated in numerous vertebrates and invertebrates (e.g., Humphreys & Ruxton 2018, Sakai 2021), but though it has long been known to occur in many ant species (e.g., Lubbock 1882, Forel 1901, Wheeler 1903, Wheeler & Gaige 1920), details about this defensive strategy are widely unknown. With our review we aim to increase the awareness of this interesting phenomenon in myrmecologists.

Many terms have been used to describe death feigning, including catalepsy, playing dead, animal hypnosis, apparent death, or thanatosis. Humphreys & Ruxton (2018) proposed to use the term "tonic immobility," as it might more accurately describe the different kinds of such behavior observed in nature and does not make any assumptions about its function and the response of predators and competitors (see also Gallup 1974, Sakai 2021). Here, we will nevertheless follow the previous usage in ants (e.g., Cassill & al. 2008, Blight & al. 2010, Bertelsmeier & al. 2015, Peters 2021, Petit & al. 2023) and refer to this phenomenon as "death feigning" (DF) to describe it in ants.

Death feigning has been intensively studied for over a century (e.g., Baskett 1893, Butler 1894, Wheeler 1901, Duporte 1916) in both vertebrates (mammals: Kimble 1997, Giannico & al. 2014; birds: Martin-Jurado & al. 2011, Spina & Silveira 2019; reptiles: Rusli & al. 2016, Bhattarai 2017; amphibians: Borges-Nojosa 2016;

fish: Tobler 2005) and invertebrates (insects: Acheampong & Mitchell 1997, Sakai 2021, Sendova-Franks & al. 2020; arachnids: Bilde & al. 2006; crustaceans: Burford & al. 2018). While for some species the physiological and neurological mechanisms associated with DF and its adaptive value have been carefully elucidated (reviewed in Humphreys & Ruxton 2018, Sakai 2021), it is still unclear how DF evolved and diversified into distinct alternatives observed across the animal kingdom. Even the phenotypic variation of death feigning and the context in which it occurs are often not well studied.

In insects, DF is observed in many orders, including Phasmatodea, Lepidoptera, Plecoptera, Hemiptera, Orthoptera, Odonata, and Coleoptera (reviewed in Cassill & al. 2008, Humphreys & Ruxton 2018). In Hymenoptera, there are reports in sawflies (Neves & Pie 2017), numerous parasitoid wasps (King & Leaich 2006, Amemiya & Sasakawa 2021), stingless bees (Van Veen & al. 1999), and several species of ants (e.g., Hölldobler & Wilson 1990). In social insects, DF may not only protect individuals against predation but may also lead to distraction and confusion among conspecific aggressors during fights for territories and resources between colonies. It might thus provide opportunities for defenders to avoid injuries and resume fighting (Humphreys & Ruxton 2018). In fact, most reports in ants report DF as a response either to experimental manipulation, for example, touching ants with forceps or opening their nest, or aggression from other ants.

DF differs from freezing and crouching, submissive behaviors often observed during dominance interactions within colonies, for example, when queens in functionally monogynous species establish social and reproductive hierarchies or when workers fight for their chance to produce males after the loss of the queen (e.g., Heinze & al. 1994, Heinze 2004). Even though subordinate individuals may remain motionless with appressed antennae and legs for many seconds even after the dominant has left, they rarely assume the typical DF postures described in Figures 1 to 3, which are exhibited by many ants during encounters with predators or competitors (but see Medeiros & al. 1992).

Data about DF in ants are scattered throughout the literature and often reported as short side notes in life history or taxonomy papers using diverse terms, such as "feign dead" (e.g., Cassill & al. 2008, Masuko 2020) or "playing dead" (e.g., Petit & al. 2023). Besides, most studies do not describe this behavior in detail or consider an evolutionary perspective. For example, though DF has been frequently mentioned in fungus-farming ants (e.g., Adams & al. 2000, 2013, 2015, Mehdiabadi & Schultz 2010), its causation or ecological context are virtually unknown, and a detailed description of DF is lacking. Furthermore, while DF in other animals is usually exhibited during interactions with a predator, ants feign death mostly in the context of nest disturbance or when attacked by other ant species. It has been suggested that DF might facilitate the co-occurrence of ant species in the same area (Grangier & al. 2007, Abril & Gómez 2009, Blight & al. 2010, Roux & al. 2013, Peters 2021) and the establishment of invasive species (Mbenoun Masse & al. 2011, Michlewicz 2022).

Here, we compile previously published information on DF in ants. We describe the types of DF exhibited by ants and outline research pathways to better elucidate this behavior, which, in consequence, might increase our understanding of DF in general.

Material and methods

Data prospecting and compilation

As a methodological basis for data collection, the guidelines contained in the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) protocol (Moher & al. 2009) were used to ensure a considerable level of standardization, bibliographic coverage, and reduction of the risk of operational bias. To structure the data, on 10 February 2022, two subsequent bibliographic searches in English in two databases each, ISI Web of Science® – Core Collection (Clarivate Analytics) and Scopus® (Elsevier), were conducted.

In the first search (extensive survey), comprehensive search terms were entered, with further refinement by related areas (see below). Thereafter, in the second search (specific survey), specific keywords were inserted separately to retrieve results missed in the first search. For both methods, the entire available chronological range of publication was used. The found references were saved in EndNoteWeb® of Web of Science. As these searches retrieved only references in which the terms were included in titles, abstracts, and keywords, a third, but less rigorous approach was conducted with Google Scholar (see details below).

Literature survey

For the extensive survey in Web of Science the terms (((TS = (dea*)) AND TS = (feig*)) OR TS = (tonic immobility)) OR TS = (thanato*) were used for a search in the Web of Science categories Agriculture Dairy Animal Science, Behavioral Sciences, Zoology, Veterinary Sciences, Genetics Heredity, Neurosciences, Psychology Biological, Biochemistry Molecular Biology, Multidisciplinary Sciences, Entomology, Ecology, Biology, Paleontology, Physiology, Evolutionary Biology, Biodiversity Conservation, Marine Freshwater Biology, Environmental Sciences, Developmental Biology, Plant Sciences, Biophysics, and Anatomy Morphology. The resulting 1501 papers were saved at <https://www.webofscience.com/wos/woscc/summary/04c84899-5a4a-4718-8bd5-28d34b69258d-2992ab81/relevance/1>. The survey in Scopus used the same search terms as above but exclusively in the category "Agricultural and Biological Sciences." This yielded 1812 articles; however, the database did not provide a public link to access the search results.

Following both extensive surveys, more specific search terms were entered separately: "dea* feig*," "feig* dea*," "play* dea*," "thanatosis," and "tonic immobility." This specific survey retrieved twelve additional results that had not been covered by the extensive surveys.

Tab. 1: Occurrence of death feigning in ants in papers retrieved by a systematic literature survey, which describe the phenomenon in some detail.

Reference	Species	Subfamily	Caste	Duration of DF	Stimuli	Location
Adams & al. (2000)	*Cyphomyrmex longiscapus* Weber, 1940	Myrmicinae	Workers	n.a.	Interspecific conflict, fight	Lab
Adams & al. (2013)	*Sericomyrmex amabilis* W.M. Wheeler, 1925	Myrmicinae	Workers	n.a.	Interspecific conflict, fight	Lab
Adams & al. (2015)	*Cyphomyrmex costatus* Mann, 1922 *Cyphomyrmex cornutus* Kempf, 1968	Myrmicinae	Workers	Very short, multiple times	Interspecific conflict, fight	Lab
Bertelsmeier & al. (2015)	*Wasmannia auropunctata* (Roger, 1863)	Myrmicinae	Workers	n.a.	Interspecific conflict, fight	Lab
Blight & al. (2010)	*Linepithema humile* (Mayr, 1868)	Dolichoderinae	Workers	Seconds after removal of the aggressor	Interspecific conflict, fight	Lab
Brandão & al. (1991)	*Thaumatomyrmex contumax* Kempf, 1975	Ponerinae	Workers	Several minutes	Indirect disturbance	Field
Brown (1974)	*Basiceros singularis* (F. Smith, 1858)	Myrmicinae	Workers	Long duration	Direct disturbance	Field
Brown (1958)	*Amblyopone australis* Erichson, 1842	Amblyoponinae	Workers	Frequent	Direct disturbance	Lab
Cardoso & al. (2016)	*Mycetophylax conformis* (Mayr, 1884) / *Mycetophylax morschi* (Emery, 1888)	Myrmicinae	Workers	n.a.	Interspecific conflict, fight	Lab
Cassill & al. (2008)	*Solenopsis invicta* Buren, 1972	Myrmicinae	Workers	n.a.	Intraspecific conflict, fight	Lab
Dobrzański (1966)	*Leptothorax acervorum* (Fabricius, 1793)	Myrmicinae	Workers	n.a.	Interspecific contact (peaceful)	Field
Grasso & al. (2020)	*Myrmecina graminicola* (Latreille, 1802)	Myrmicinae	Workers	Several seconds	Direct disturbance and Interspecific contact	Field and Lab
Katayama (2013)	*Discothyrea kamiteta* Kubota & Terayama, 1999	Proceratiinae	Workers, queen	~ 60 seconds (queen), several seconds (workers)	Direct disturbance	Lab
Kutter (1951)	*Temnothorax stumperi* (Kutter, 1950)	Myrmicinae	Queens	Short	Interspecific contact	Field
Langen & al. (2000)	*Pheidole gilvescens* Creighton & Gregg, 1955	Myrmicinae	Workers	Seconds after the removal of aggressor	Intra- and Interspecific conflict, fight	Lab
Mbenoun Masse & al. (2011)	*Wasmannia auropunctata*	Myrmicinae	Workers, queen	Queens: 5.50 ± 0.86 seconds Workers: 2.96 ± 0.90 seconds	Indirect disturbance	Lab
Mehdiabadi & Schultz (2010)	*Sericomyrmex* spp., *Trachymyrmex* spp.	Myrmicinae	Workers	n.a.	Direct disturbance	n.a.
Schumacher & Whitford (1974)	*Trachymyrmex smithi* Buren, 1944	Myrmicinae	Workers	~ 3 minutes	Direct disturbance, interspecific contact	Field
Sosa-Calvo & al. (2017)	*Apterostigma megacephala* Lattke, 1999	Myrmicinae	Workers	Several minutes	Direct disturbance	Field
Weber (1958)	*Cyphomyrmex rimosus* (Spinola, 1851)	Myrmicinae	Workers	n.a.	Direct disturbance	Field
Wheeler (1901)	*Leptothorax canadensis* Provancher, 1887	Myrmicinae	Workers	n.a.	Direct disturbance, interspecific contact	Field
Wheeler & Gaige (1920)	*Cryptopone gilva* (Roger, 1863)	Ponerinae	Workers	Several seconds	Direct disturbance	Field
Wilson (1956)	*Eurhopalothrix biroi* (Szabó, 1910)	Myrmicinae	Workers	n.a.	Interspecific contact	Lab

EndNoteWeb and inclusion criteria

The sum of all results was subjected to EndNoteWeb duplicate scanning, leaving 3132 articles. Subsequently, all titles, keywords, and abstracts were inspected visually, resulting in a final list including only those publications that reported the occurrence of death feigning, pretending to be dead, thanatosis, tonic immobility, or other variations of the terminology in at least one ant taxon or mentioning its occurrence in Formicidae. Only 23 of 3132 articles met these criteria. The results extracted from these articles are shown in Table 1. In addition to details of the reference, information is given on the duration of the behavior, the caste exhibiting it, whether the observation was made in the laboratory or the field, and what triggered the behavior. Based on this table, basic statistics were calculated using Macintosh Numbers™ 11.0 tools.

Due to the limited number of studies available and the heterogeneity in which the data were reported, it was impossible to conduct a statistical metanalysis with significant support. Thus, all articles recovered were fully read and a qualitative review was carried out based on the information compiled from the studies gathered.

While the analysis of DF focused on the 23 reports retrieved in the systematic literature surveys described above, Google Scholar and printed papers in our libraries were searched for additional reports of DF in the full texts to better document the occurrence of this phenomenon in ants. This more than doubled the number of papers mentioning DF. Though the search focused mostly on papers in English, searching the web with terms from other languages (thanatose, tanatosis, tanatosi, Totstellen, faire le mort, hacerse el muerto, muerte simulada) yielded only few additional anecdotal reports, mostly in papers that are not listed in online databases.

Analytic results

Quantitative and general considerations about death feigning in ants

Taken together, our systematic and opportunistic surveys retrieved approximately 65 reports on DF in ants. Most of these reports were short anecdotal mentions (e.g., Taylor 1978, Mei 1995, Lacau & al. 2003), and only four, that is, Grasso & al. (2020), Mbenoun Masse & al. (2011), Peters (2021), and, to a lesser extent, Katayama (2013), presented information on duration, conditions, and context in which DF was observed as well as characteristics of individuals exhibiting it, such as caste and age (see Tab. 1). Note that Table 1 only covers references found in the systematic survey and does not contain Peters (2021), as this unpublished Ph.D. thesis is not listed in the databases.

From the limited information available, it is possible to infer that DF occurs in a wide range of genera and that the duration of DF is typically a few seconds to a maximum time of a few minutes. Also, workers appear to be the caste most frequently observed exhibiting this behavior (see Tab. 1).

Occurrence of death feigning across the Formicidae

Death feigning after nest disturbance, during intraspecific fights or interspecific contact has been reported from at least nine subfamilies of ants, including Amblyoponinae (Brown 1958), Dolichoderinae (e.g., Blight & al. 2010, Trigos-Peral & al. 2021), Ectatomminae (Cupul-Magaña 2009), Formicinae (Abril & Gómez 2009, Petit & al. 2023), Heteroponerinae (Wheeler 1923), Myrmeciinae (Taylor 1978), Myrmicinae (e.g., Mehdiabadi & Schultz 2010, Grasso & al. 2020, Peters 2021), Ponerinae (Wheeler & Gaige 1920, Brandão & al. 1991, Rakotonirina & Fisher 2013a), and Proceratiinae (Katayama 2013, Masuko 2020). This parallels its wide occurrence in other animals: As Humphreys & Ruxton (2018) concluded, DF can easily evolve because it is simply a "lack of behavior" that does not require special adaptations.

DF has anecdotally been reported in numerous well-known ant taxa (*Acromyrmex*: Jutsum 1979, *Atta*: Roux & al. 2013, *Formica*: Le Moli & Mori 1989, *Leptothorax*: Dobrzański 1966, *Linepithema humile*: Blight & al. 2010, *Monomorium*: Rao & Vinson 2009, *Pheidole*: Langen & al. 2000, *Polyrhachis*: Petit & al. 2023, *Solenopsis invicta*: Cassill & al. 2008, *Temnothorax*: Wheeler 1903, *Tetramorium*: O'Rourke 1950, Mei 1995, Guillem & Bensusan 2009, Peters 2021), while we did not find references involving other commonly studied genera, including *Camponotus*, *Cardiocondyla*, *Cataglyphis*, *Lasius* (but see Kannowski 1959), *Myrmica*, and *Oecophylla*.

Our literature search suggests an uneven distribution of reports, with most detailed observations from the Myrmicinae, and here particularly from the fungus-farming ants. With exception of the leaf-cutting ant genera *Atta* and *Acromyrmex*, fungus-farming ants are commonly characterized by their non-aggressive behavior (e.g., Weber 1958, Adams & al. 2000, 2013, 2015, Mayhé-Nunes & Brandão 2007, Mehdiabadi & Schultz 2010, Cardoso & al. 2016). In particular, many of the more basal, non-leaf-cutting species are small and lack defensive structures, such as a potent sting (Kugler 1979). They are quite "timid" and have cryptic coloration (Mehdiabadi & Schultz 2010, Sosa-Calvo & al. 2015, 2017), which potentially contributes to a greater tendency to exhibit DF to avoid or minimize attacks or injuries from aggressive ants and other natural enemies. Furthermore, in these ants, but also in other genera with DF, such as *Meranoplus, Cataulacus*, or *Stegomyrmex* (Arnold 1917, Hölldobler & Wilson 1986), morphological structures, such as antennal scrobes or expanded frontal lobes, appear to protect vulnerable parts of the body in this defensive posture (Mehdiabadi & Schultz 2010, Anderson 2006; Fig. 1).

Individuals in several other genera, for which DF has been mentioned at least in some species (*Basiceros*: Brown 1974, *Eurhopalothrix*: Wilson 1956, *Hylomyrma*: Ulysséa & Brandão 2021, *Indomyrma*: Brown 1985, *Leptothorax*: Dobrzański 1966, *Lordomyrma*: Taylor

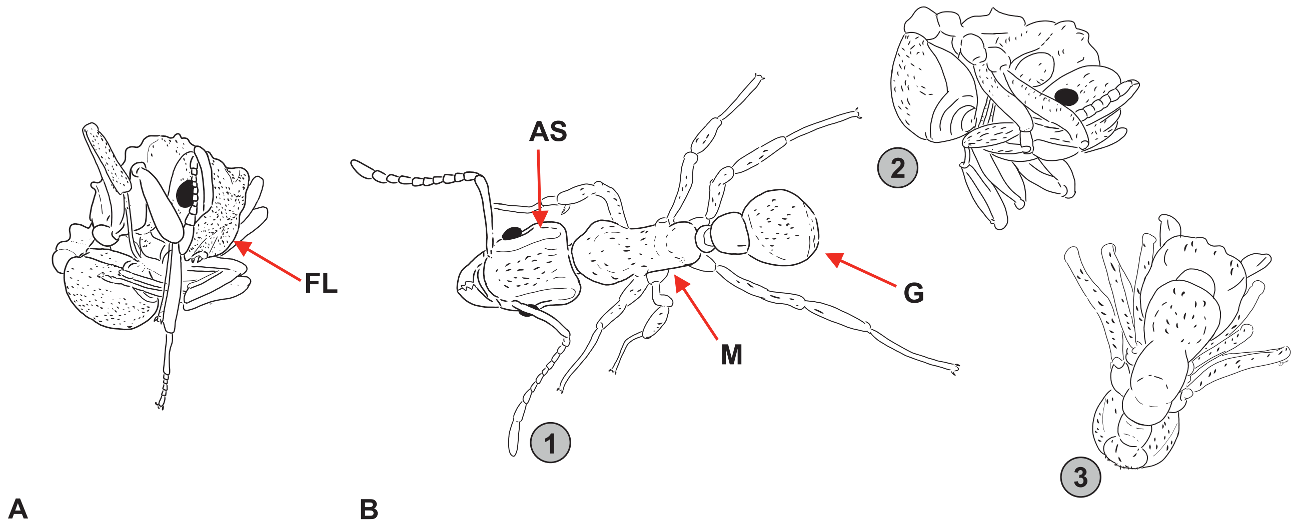

Fig. 1: A) *Cyphomyrmex transversus* (collected in Dunas beaches – Cabo Frio, Rio de Janeiro) performing death feigning (lateral view). The heads of the workers of this species are characterized by a marked groove and an expansion of the frontal lobes (FL). B) *Mycetophylax morschi* (collected in Morro dos Conventos – Araranguá, Santa Catarina) in walking posture (1) and DF posture in lateral (2) and dorsal (3) view. This species also presents an antennal scrobe (AS) although it is less pronounced than in *C. transversus*. (M) mesosoma, (G) gaster. Drawn by Danon C. Cardoso.

2012, *Melissotarsus*: Bolton 1973, *Octostruma*: Palacio 1997, *Plagiolepis*: Abril & Gómes 2009, *Stenamma*: Smith 1957, Branstetter 2012, *Temnothorax*: Wheeler 1903), are also small, cannot easily defend themselves against larger competitors, and tend to behave submissively during encounters with other ant species. Cryptic coloration and soil-binding pilosity, as in *Strumigenys* (Munsee 1976, Lacau & al. 2003, Michlewicz 2022), *Basiceros,* and *Stegomyrmex* (Hölldobler & Wilson 1986, Wilson & Hölldobler 1986, Diniz & Brandão 1993), may add to the inconspicuousness of death-feigning ants (Dornhaus & Powell 2009).

Nevertheless, species that are dominant and aggressive in native or introduced populations, such as *Tetramorium caespitum* (see O'Rourke 1950), *Solenopsis invicta* (Cassill & al. 2008), *Linepithema humile* (see Blight & al. 2010), or *Wasmannia auropunctata* (see Feitosa 2007, Bertelsmeier & al. 2015), may also employ DF at least in particular situations.

The occurrence of DF may vary even among closely related genera. While workers of *Paratrachymyrmex diversus* practically never exhibit DF and react aggressively to attacks and threats (Schultz & Meier 1995), many workers of *Trachymyrmex smithi* express this behavior (Schumacher & Whitford 1974). The same discrepancy was observed in escalating fights between two seed-harvesting *Pheidole* species: *P. gilvescens* performed DF, while this was never observed in *P. tucsonica* (see Langen & al. 2000). According to Rakotonirina & Fisher (2013a,b), DF is exhibited only in one of two morphologically similar genera of Malagasy Ponerinae, which readily allows to distinguish between them in the field.

Appearance of death feigning in ants

According to Humphreys & Ruxton (2018), death feigning animals become motionless after contact with a predator or another potentially dangerous object and remain immobile for a while without reacting to external stimuli even after the contact has ended. In ants, individuals feigning death either flip onto their backs or, more commonly, curve ventrally with retracted legs and antennae. These postures are promptly assumed during the disturbance and retained for several seconds to minutes. Both closely resemble the postures observed in ant corpses.

In the first type of DF, the ant raises the ventral side of its body and lowers its back with the help of its legs and stops moving. While the antennae are not retracted, the legs may be so to some extent (e.g., *Myrmicocrypta* sp., Fig. 2). In the second type, the ants assume a crouched, pupa-like posture with head and legs flexed toward the mesosoma and the gaster bent ventrally (Figs. 1, 3; e.g., Attini: Mehdiabadi & Schultz 2010; *Nothomyrmecia macrops*: Taylor 1978; *Plagiolepis pygmaea:* Abril & Gómez 2009; *Ectatomma ruidum*: Cupul-Magaña 2009; *Meranoplus* spp.: Hölldobler 1988). The degree of body curvature and the retraction of legs may vary considerably. The three most common postures are (1) closed, that is, head and abdomen curved maximally towards the center of the body, legs bent towards the center and parallel to the bilateral axis (e.g., *Mycetophylax morschi, Myrmecina graminicola, Discothyrea kamiteta*); (2) intermediate, that is, similar to the closed posture but legs, although retracted towards the center, being positioned more diagonally to the bilateral axis (e.g., *Cyphomyrmex* sp.), and (3) open, that is, head and abdomen less curved and legs bent to

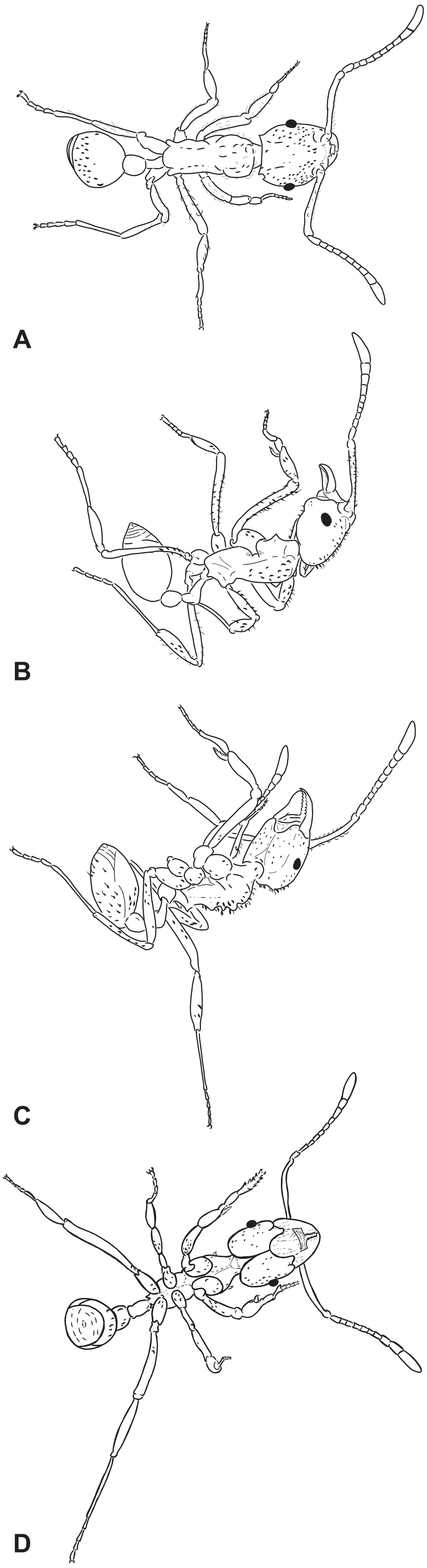

Fig. 2: Schematic representation of death feigning flipping onto its back observed in *Myrmicocrypta* sp. (collected in Dunas beaches – Cabo Frio, Rio de Janeiro). After disturbance, A) the ant stops walking, B) begins to retract the legs on one side of the body, then C) extends the hind- and forelegs to turn around, and D) becomes immobile with its ventral body side up and the dorsum down. Drawn by Danon C. Cardoso.

the center and parallel to the bilateral axis (*Solenopsis invicta*). These three postures and their variations are likely not the only DF postures assumed by ants.

As has been shown in other insects, different stimuli may imply different ways of displaying DF and also affect its propensity and duration. For example, some Colorado potato beetles, *Leptinotarsa decemlineata*, needed more time to recover from DF when a vibratory stimulus was repeated, while others habituated to the stressor (Acheampong & Mitchell 1997). Furthermore, DF may vary with age and physiological status: Older females of the parasitoid wasp *Heterospilus prosopidis* feign death longer than younger females (Amemiya & Sasakawa 2021). The opposite was the case in the weevil *Cylas formicarius* (see Kuriwada & al. 2011), and both females and males reduced the duration of DF after copulating (Kuriwada & al. 2009). In ixodid ticks, starved individuals feigned death for a shorter time than fed individuals when grasped with forceps (Oyen & al. 2021).

In ants, individuals from the same colony may also need stimuli of different intensity before exhibiting DF (O'Rourke 1950, Schumacher & Whitford 1974, Cassill & al. 2008, Peters 2021), but the causes of this variation have rarely been investigated. One factor may be caste: Two studies reported that queens exhibit DF longer than workers (*Wasmannia auropunctata* queens: 5.50 ± 0.86 standard deviation, SD, seconds, workers 2.96 ± 0.90 SD seconds when placed into new experimental arenas, Mbenoun Masse & al. 2011; *Discothyrea kamiteta* queen: 60 sec vs. workers "a few seconds" when touched by forceps, Katayama 2013). Concerning sex, DF has not yet been observed in males.

The importance of individual age has so far been studied only in *Solenopsis invicta* (Cassill & al. 2008): While older workers responded to aggression by fleeing or fighting back, days-old workers with a still soft cuticula readily exhibited DF. It is likely that in other species age may similarly effect on whether an individual exhibits DF in response to an attack or reacts aggressively.

Context of death feigning in ants

The prevalence of laboratory observations (Tab. 1) reflects the difficulty of studying this type of behavior in the field. In most studies, DF was elicited in the lab either by experimental manipulation or in interactions with other ants in staged encounters. In the first case, individuals were directly or indirectly disturbed with forceps by touching the ant or the nearby substrate. Biological interactions included both inter- and intra-specific contact in small arenas between few or many individuals. While the systematic survey yielded only four studies in which DF was reported in a natural environment and without intentional provocation (Dobrzański 1966, Schumacher & Whitford 1974, Brandão & al. 1991, Grasso & al. 2020), the additional search revealed other cases, for example, when nests were opened or disturbed in the field (e.g., Mei 1995, Lacau & al. 2003, Rakotonirina & Fisher 2013a, Petit & al. 2023). In contrast to other animals,

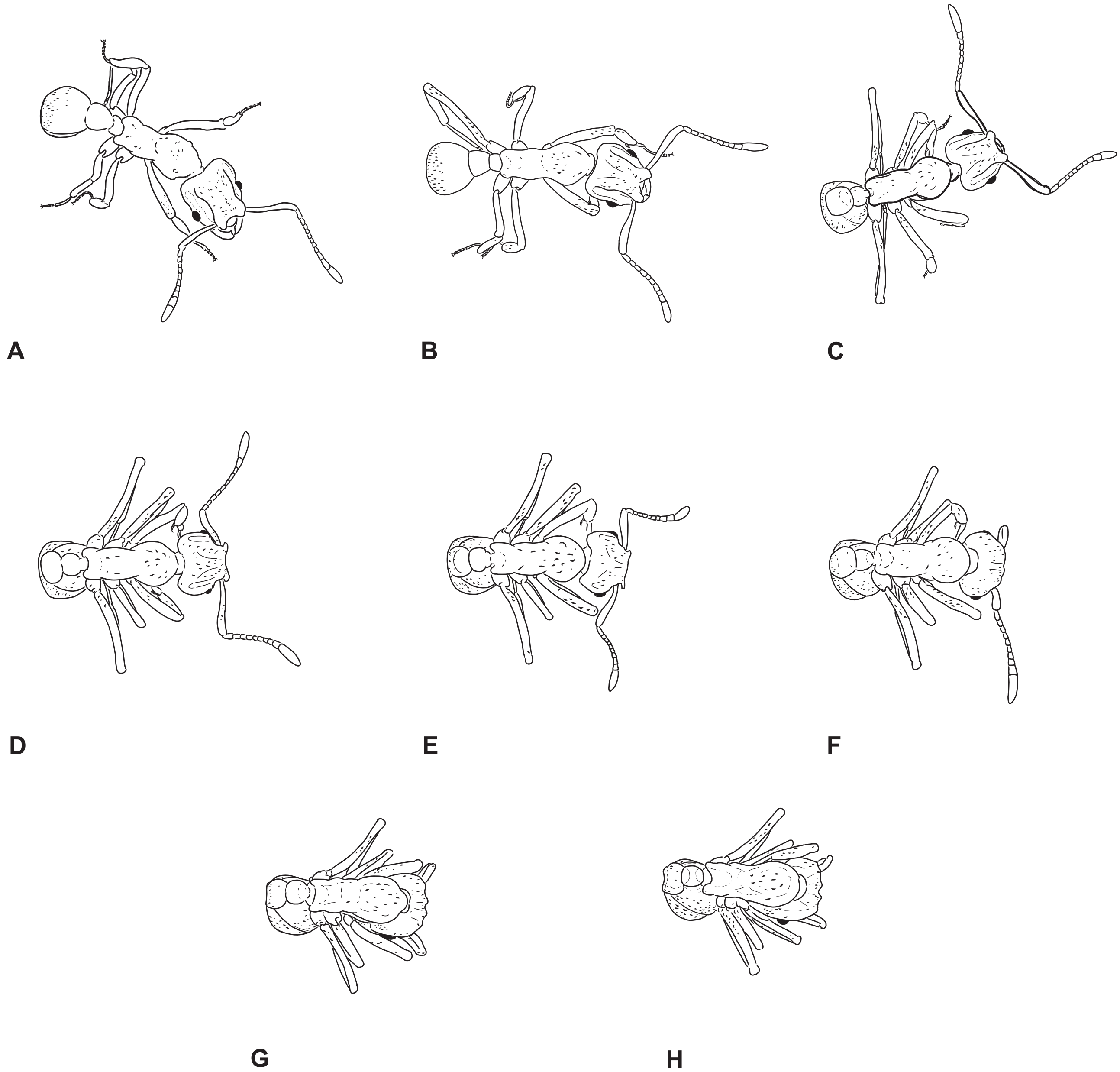

Fig. 3: Schematic representation of death feigning by curving ventrally and retracting appendices (legs and antennae) observed in *Mycetophylax morschi* (collected in Morro dos Conventos – Araranguá, Santa Catarina). After disturbance, A) the ant starts retracting its hindlegs, followed by B) the retraction of the middle legs and an initial curling of the gaster. This progresses in C) with the initial retraction of forelegs, D) culminating in a "closed-open" posture, in which the legs are held ventrally and E) the gaster is almost fully curled. F) One antenna is folded into the scrobe, G) followed by the other antenna and ventral curving of the head. H) Finally, the gaster is maximally curled, the legs are tightly retracted, and head and antennae are in a ball-like, immobile posture. Drawn by Danon C. Cardoso.

in which DF is exhibited to avoid being eaten (Honma & al. 2006, Humphreys & Ruxton 2018, Sakai 2021), DF has rarely been documented in response to an ant-eating predator.

Death feigning was often shown by submissive ant species during encounters with more dominant, aggressive ants to avoid being bitten, grasped, or stung (Jutsum 1979, Rao & Vinson 2009, Blight & al. 2010, Bertelsmeier & al. 2015, Cardoso & al. 2016, Grasso & al. 2020, Langen & al. 2000), and may also occur during intraspecific territorial disputes (e.g., Cassill & al. 2008). While DF is most commonly exhibited by weaker, attacked individuals and presumably serves to lessen or avoid aggression, workers of the dominant *Wasmannia auropunctata* also occasionally exhibited DF, perhaps using it as a tactic to confuse the enemy (Bertelsmeier & al. 2015). DF is not necessarily a completely passive strategy: Stäger (1925) concluded from the observation of extruded stings in death feigning *Formicoxenus nitidulus* that the apparently lifeless ant is indeed preparing to aggressively defend itself.

Inside the nest, DF has been observed as a reaction of the fungus-farming genera *Sericomyrmex* and *Cyphomyrmex* when aggressive *Megalomyrmex* and *Gnamptogenys* raided their fungus gardens (Adams & al. 2000, 2013, 2015). On the contrary, DF can also be employed by the usurper when trying to infiltrate a host nest. Queens of several socially parasitic ants exhibit DF when approached by host workers (*Temnothorax stumperi* – also referred to as *Myrmoxenus stumperi*, see Kutter 1951; *Leptothorax pacis*, see Kutter 1969; *Formica pressilabris*, see Kutter 1957; *Lasius speculiventris*, see Kannowski 1959). DF has also been reported for a number of ant guests, for example, beetles and other arthropods living in the nests of ants (e.g., Wheeler 1908, Hölldobler & al. 1981, Wojcik & Naves 1992), as well as for *Formicoxenus* guest ants (Stumper 1919, Stäger 1925).

Finally, in species of *Discothyrea*, specialized predators of spider eggs, DF might be an adaptation to avoid being detected by the egg-guarding mother spider (Katayama 2013, Masuko 2020). Other spider egg-eating ants, such as *Stictoponera menadensis* (see Brown 1947) and *Proceratium gibbosum* (see Sadasivan & Kripakaran 2022), have also been observed to exhibit DF upon disturbance.

Experimentally, DF can often be induced by mere touch with forceps, while other species require repetitive contacts for several minutes (e.g., Wheeler 1901, Schumacher & Whitford 1974). *Polyrhachis femorata* (see Petit & al. 2023) exhibited DF already when their artificial nest box was opened, and members of the *Bothroponera wasmannii* group also feigned death when their nests were disturbed (Rakotonirina & Fisher 2013a). Our data matrix (Tab. 1) shows an approximately equitable distribution of different stimuli causing DF, mostly artificial disturbance or contact with other individuals under laboratory conditions. However, details on how the ants were actually disturbed and how the ants reacted to varying disturbance are rarely given. One exception is the study by Grasso & al. (2020), who induced DF in workers of *Myrmecina graminicola* by four types of mechanical disturbance, varying from light to strong touch with a plastic rod or forceps. Those stimuli that caused a more intense loss of contact with the substrate led to a longer duration of DF, and there also was a clear correlation between the type of DF and the context in which it was induced. In a second study, Cassill & al. (2008) compared the reaction of workers of *Solenopsis invicta* to contact with conspecific ants, allospecific ants, and touch with the hairs of a paint brush. Young workers exhibited DF during encounters with other ants, but not in response to being touched with a brush.

Reaction to death feigning in ants

DF is typically seen as a last resort to survive an attack when fleeing or fighting back are futile (e.g., Rogers & Simpson 2014, Humphreys & Ruxton 2018, Sakai 2021). Indeed, in many observations, aggressors reacted to DF in ants by stopping their attack (e.g., Abril & Gómez 2009) and quickly lost interest in the immobile individual (Dobrzański 1966, Grangier & al. 2007). Workers of *Tapinoma nigerrimum* were even observed to carry death-feigning workers of *Linepithema humile*, which had intruded into their territory, to their own cemetery (Blight & al. 2010). Cassill & al. (2008) reported that young workers of *Solenopsis invicta*, which exhibited DF when attacked, had a four times higher survival rate than older workers, which fought back or fled.

However, DF is not always successful: When raiding fungus-farming colonies, *Gnamptogenys hartmani* invaders locked on to their *Sericomyrmex amabilis* opponents and continued to sting them even though the latter displayed DF (Adams & al. 2013). Stings and biting were also used by *Megalomyrmex* against death feigning *Cyphomyrmex longiscapus* (see Adams & al. 2000) and on *Mycetophylax conformis* and *Mycetophylax morschi* (see Cardoso & al. 2016). More research is necessary to fully comprehend what drives some ants to continue to attack or to be indifferent to their death-feigning opponents.

Conclusion and perspectives

Our review shows that death feigning in ants, though frequently reported, has rarely been studied in detail. Basic information, for example, about the duration of DF under different stimuli, is missing, and whether and how the prevalence of DF varies with the type of threat, caste, age, task group, or "personality" is largely unknown. These and several other potential research topics are outlined in Table 2 with suggestions for how to investigate DF in particular contexts and which species to use as model systems.

The limited knowledge about DF in ants contrasts conspicuously with the surprisingly large number of detailed studies on this phenomenon in other animals, for example Coleoptera (e.g., Humphreys & Ruxton 2018 and references therein), in which physiological and neurological correlates of DF and even its heritability have been studied. For example, in *Tribolium* beetles, DF appears to be part of a heritable behavioral syndrome negatively correlated with activity levels (Prohammer & Wade 1981, Nakayama & al. 2010, Uchiyama & al. 2019). Furthermore, the situations in which DF occurs and how strongly it increases survival have also often been quantified (e.g., Rogers & Simpson 2014; Humphreys & Ruxton 2018). In contrast, in ants it presently remains unclear whether DF is ever a successful strategy against ant-eating predators, and its purpose often remains dubious even in the context of interactions between or within ant species, as indicated by Adams & al. (2000, 2013) (Tab. 2). Curling up in a pupa-like posture might indeed not always be a defense against the opponent, but could make it easier for less vulnerable nestmates to pick up and carry young individuals away from the dangerous zone (e.g., Frank & al. 2017). Alternatively, in the case of fungus-growing ants, DF might make it more difficult for the attacker to eliminate the defender and thus increase the "handling time", allowing its nestmates to rescue parts of the fungus garden and the brood (but see Adams & al. 2000).

Tab. 2: Open research topics on death feigning in ants. We highlight some of the questions, taxa studied, the experimental methodology, and source when available.

Open research questions	Taxa to be studied	Methodology	Literature
Are there ant taxa that never exhibit DF?	*Camponotus*, *Cardiocondyla*, *Cataglyphis*, *Myrmica*, *Oecophylla* and others.	Field or laboratory observation in encounters with predators, other ants, or experimental manipulation using forceps	
Is DF ever exhibited against ant-eating predators and if so, is it successful?	In particular those taxa in which DF is regularly observed (e.g., fungus-farming ants or *Myrmecina*)	Preferably field observations with natural predators, such as birds, spiders, etc.	e.g., GRASSO & al. (2020)
How reliably does DF stop an aggressive attack?	In particular those taxa in which DF is regularly observed (e.g., fungus-farming ants or *Myrmecina*)	Staged encounters with aggressive ants in the field or laboratory, preferably both close to and away from the natal nest of the death-feigning ant	ADAMS & al. (2000, 2013)
Does DF by introduced ants lead to a stable coexistence with aggressive, native ants? Is DF more frequently shown in newly colonized areas?	Less aggressive introduced species, such as *Strumigenys emmae* or *Vollenhovia emeryi*	Comparison of the occurrence of DF in staged laboratory encounters with more aggressive ants in both native and introduced populations	MBENOUN MASSE & al. (2011), PETERS (2021), MICHLEWICZ (2022)
Does DF vary with individual age or individual and colony "personality"?	Any taxa with DF	Experimental manipulation of workers of known age or known "personality" in the laboratory	e.g., CASSILL & al. (2008), PINTER-WOLLMAN (2012), HORNA-LOWELL & al. (2021)
Is DF associated with other defense mechanisms, e.g., chemical secretions ?	Any taxa with DF	Comparison of chemical profiles of ants exhibiting DF and controls	For the red flour beetle, *Tribolium castaneum* see MIYATAKE & al. (2009)
Does DF exhibited by queens differ from that exhibited by workers in posture or duration, and if so, what is the benefit of this difference?	Any taxa with DF	Comparison between the castes under controlled conditions in the laboratory	MBENOUN MASSE & al. (2011), KATAYAMA (2013)
Do males ever exhibit DF and in which situations?	Any taxa in which male behavior can be studied in the laboratory	Behavioral observations of male behavior, e.g., during competition with other males in mating flights or encounters with workers from other colonies	

The frequent observation of DF in encounters between competing species suggests that it facilitates the coexistence of submissive and dominant ants (e.g., GRANGIER & al. 2007, ABRIL & GÓMEZ 2009, BLIGHT & al. 2010, ROUX & al. 2013, PETERS 2021) and may also allow the establishment of invasive species in a new environment, as in the case in *Wasmannia auropunctata* (see MBENOUN MASSE & al. 2011) and *Strumigenys emmae* (see MICHLEWICZ 2022). For example, DF might help invasive species to avoid being attacked and expelled from the territories of native ants. However, more detailed investigations about whether and how DF facilitates permanent coexistence, in particular between native and invasive taxa, are needed. It might also be of interest to see whether the probability of exhibiting DF differs between native and introduced populations of the same species (Tab. 2).

To conclude, our review provides evidence for the wide distribution of DF across ants, but many questions about its occurrence, benefits, and costs are still open (Tab. 2). We hope that our review will inspire more research on this phenomenon, which essentially is easy to investigate without complex equipment.

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