



Brood recognition and discrimination in ants

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Received: 25 July 2019 / Revised: 3 December 2019 / Accepted: 21 December 2019 / Published online: 22 January 2020
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Abstract

In social insect colonies, individuals need to communicate to coordinate cooperative tasks and protect the colony and its resources against intruders. To maintain colony integrity, it can be particularly important to recognize nestmates and discriminate against non-nestmate conspecifics and heterospecific predators and parasites. As typical intruders are either con- or heterospecific adults, the mechanisms underlying recognition and discrimination processes in interactions among adults have been well described. Ant brood (eggs, larvae, and pupae) can also play a key role in social interactions, and brood is of special importance when it comes to the priorities of worker ants. However, whether ants can, or even need to, recognize brood of different origins, is not always clear. In this review, we integrate the results of 100 years of study on brood recognition and discrimination in ants into a general framework. We begin with an overview of the proximate mechanisms involved in brood recognition and discrimination. We then discuss why brood recognition and discrimination should evolve and review the evidence for brood recognition on three organizational levels: within nests, between conspecifics and between species. We conclude by examining the constraints acting on accurate recognition and/or discrimination. With this review, we hope to inspire future research on the fascinating life of ant brood.

Keywords Social insects · Inclusive fitness · Behavior · Cuticular hydrocarbons · Pheromones · Pupae · Larvae · Eggs

Introduction

Ants need to assess their social environment and communicate with nestmates to coordinate cooperative processes such as reproductive division of labor, foraging, and brood care. Communication is also crucial for protecting the colony and its resources from exploitation by unrelated conspecific and heterospecific predators and parasites. Mechanisms of task-related communication and nestmate and intruder recognition and discrimination have been well reviewed in adult ants (d’Ettorre and Lenoir 2010; van Zweden and d’Ettorre 2010; Sturgis and Gordon 2012; Tsutsui 2013; Czaczkes et al. 2014; Leonhardt et al. 2016), and mainly rely on two kinds of chemical signals: glandular secretions and mixtures of hydrocarbons on the body surface (Vander Meer et al.

1998; Martin and Drijfhout 2009a; Blomquist and Bagnères 2010; van Wilgenburg et al. 2011). Hydrocarbons are produced in specialized cells (oenocytes) and then transported to the cuticle, where they form a waxy layer that prevents desiccation (Gibbs 1998; Gibbs and Rajpurohit 2010). In many insects, including ants, hydrocarbons have secondarily evolved a function in communication (Blomquist and Bagnères 2010; Chung and Carroll 2015).

Adult ants from the same nest share a hydrocarbon profile, which is partly inherited (Drescher et al. 2010; van Zweden et al. 2010; Nehring et al. 2011; Helanterä and d’Ettorre 2014) and partly shaped by an individual’s nutritional and social environment (Soroker et al. 1995; Dahbi et al. 1999; Lenoir et al. 2001a; Foitzik et al. 2007; van Zweden et al. 2009a; Bos et al. 2011). In addition to their species and colony specificity (e.g., Martin et al. 2008a, b), adult hydrocarbon profiles can change with age (Cuvillier-Hot et al. 2001; Teseo et al. 2014), reflect fecundity (Peeters et al. 1999; Liebig et al. 2000; Cuvillier-Hot et al. 2001, 2004; Dietemann et al. 2003, 2005; Holman et al. 2010; Will et al. 2012), and differ among body parts (Wang et al. 2016), task groups (Wagner et al. 1998, 2001; Martin and Drijfhout 2009b; Larsen et al. 2016),

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sexes (Cuvillier-Hot et al. 2001; Kleeberg et al. 2017), and castes (Monnin 1999; Kleeberg et al. 2017). In addition to chemical cues, adult ants can also communicate using acoustic (reviewed in Schönrogge et al. 2017) and visual cues (Hölldobler and Wilson 2009).

Although often overlooked, ant brood (i.e., eggs, larvae, and pupae) play a key role in social interactions (Schultner et al. 2017) and are of special importance when it comes to the decisions and motivation of workers. Ant workers show directed behavior towards brood (Wilson 1971) and retrieving and tending brood is the main priority of a worker ant; even tending to the queen is secondary (Lenoir 1981). This is exemplified by the fact that after disturbance to a colony, the first thing workers do is secure brood (Haskins and Haskins 1950; Lenoir 1981; Muscedere et al. 2009; Römer and Roces 2014). The adaptive advantages of recognizing brood as such are obvious: worker responsiveness to brood is necessary for efficient brood care, which is in the interest of all colony members, because brood represents a colony's combined reproductive investment. As growth and development of ant brood are tightly linked to brood care behavior by workers (Linksvayer 2007, 2008), recognizing and discriminating brood according to traits such as developmental stage, sex, caste, maternity, kinship, colony, population, and species may be selected if it allows colonies to optimize fitness-related processes such as the production of sexual offspring.

In this review, we integrate the results of 100 years of study on brood recognition and discrimination in ants into a general framework. The first review on this topic by Carlin (1988) referenced about 30 empirical studies. Since then, 83 studies have examined worker (and sometimes queen or larva) discriminatory behavior towards brood of different developmental stages, sexes, castes, maternities, kinships, colonies, populations, and species. Some of these studies also investigated the underlying cues used for discrimination. We include, to the best of our knowledge, all references published on this topic, irrespective of publication year (see Tables 1, 2, 3 and references therein). We loosely structure our review along the four principles for the study of behavior: causation, ontogeny, adaptive value and phylogeny (Tinbergen 1963). In the section “**Brood recognition: how?**”, we treat the questions of causation and ontogeny by giving an overview of the proximate mechanisms involved in brood recognition and discrimination. In the section “**Brood recognition: why?**”, we discuss the adaptive value of accurate brood recognition and discrimination and review the evidence for discrimination on three organizational levels (within nests, between conspecifics, and between species). We conclude by examining the ecological and experimental constraints that influence accurate recognition and discrimination, or detection thereof. In each section, we present avenues of future research that will help resolve open questions about brood discrimination in ants.

Brood recognition: how?

Recognition systems typically have three components. The sender produces or bears a stimulus that relates to a relevant trait (expression component). The receiver perceives this stimulus and integrates the information (perception component). The receiver then responds to the sender according to the information gathered from the stimulus (action component). Thus, recognition does not always imply action, but action requires recognition. Recognition is used to describe the neural process associated with assessing the phenotypes of social partners (Waldman 1987), for instance, by reacting to stimuli encoded by genotype or based on context (e.g., shared nest) or prior association. Discrimination is used to describe the differential treatment of social partners following phenotype perception. The majority of studies focus on discrimination, since this is more easily measured than recognition. Here, we use “recognition” when we address the stimuli associated with different phenotypes and “discrimination” when we discuss differential behavior towards individuals of different phenotypes.

Both senders and receivers are critical actors in recognition systems (Fig. 1). In the context of brood recognition and discrimination, brood typically act as senders, while workers act as receivers (although some studies have also tested the recognition and discrimination abilities of queens and larvae, see Tables 1, 2, 3). We begin the first section of this review by examining how brood can transmit information. We then review the current state of knowledge concerning the ontogeny of this behavior in workers.

Brood recognition cues

Recognition and discrimination are based on the assessment of stimuli in the form of cues or signals. The term “signal” is used for stimuli which have specifically evolved to convey information from sender to receiver, while the term “cue” denotes any stimulus used by the receiver, even if this stimulus did not evolve to function in a communication context (Maynard Smith and Harper 2003). Defining a given stimulus as a signal rather than a cue requires careful testing of the action and function of said stimulus and, in the case of chemical stimuli, a synthetic version, using appropriate behavioral experiments. As such comprehensive studies of brood recognition are rare, we refer to brood recognition stimuli as cues throughout this review, with the exception of queen-borne odors on eggs (i.e., queen pheromones), which have been identified as species-specific signals that have evolved to convey information about queen fertility (Holman et al. 2010; Van Oystaeyen et al. 2014).

Table 1 Overview of studies conducted on ant brood recognition and discrimination in the context of within-nest interactions

Discrimination context	Development stage	Species	Evidence for discrimination	Recognition cues used	References
Worker-laid vs. queen/gamergate-laid	Egg	<i>Aphaenogaster smythiesi japonica</i>	Yes		Iwanishi et al. 2003
		<i>Camponotus floridanus</i>	Yes	Egg odor	Endler et al. 2004
		<i>Dinoponera quadriceps</i>	Yes	Egg odor	Monnin and Peeters 1997
		<i>Formica selysi</i>	Yes		Meunier et al. 2010
		<i>Myrmecia gulosa</i> (queen)	Yes	Egg odor	Dietemann 2002; Dietemann et al. 2005
		<i>Leptothorax acervorum</i> (queen)	No		Bourke 1991
		<i>Novomessor cockerelli</i>	No		Smith et al. 2008a
		<i>Temnothorax unifasciatus</i>	No		Stroeymeyt et al. 2007
		<i>Neoponera inversa</i>	Depends on queen presence, brood origin	Egg odor	d’Ettorre et al. 2004, 2006; van Zweden et al. 2007, 2009b
		<i>Formica fusca</i>	Depends on queen presence		Helanterä and Sundström 2005, 2007; Helanterä and Ratnieks 2009a
		<i>Diacamma sp.</i> (gamergate)	Depends on caste of discriminator	Egg odor	Nakata and Tsuji 1996; Kikuta and Tsuji 1999; Shimoji et al. 2012
		Queen fertility	Egg	<i>Camponotus floridanus</i>	Yes
Male vs. female	Egg, larva, pupa	<i>Formica selysi</i> ^(?)	Yes		Rosset and Chapuisat 2006
		<i>Lasius niger</i> ^(L)	Yes		Jemielity and Keller 2003
		<i>Myrmica rubra</i> ^(L)	Yes		Brian and Carr 1960; Brian 1981
		<i>Myrmica tahoensis</i> ^(L)	Yes		Evans 1995
		<i>Pheidole pallidula</i> ^(?)	Yes		Keller et al. 1996
		<i>Plagiolepis pygmaea</i> ^(L)	Yes		Aron et al. 2004
		<i>Solenopsis invicta</i> ^(?)	Yes		Aron et al. 1995
		<i>Leptothorax acervorum</i> ^(E)	No		Hammond et al. 2002
		<i>Camponotus floridanus</i> ^(P)	Depends on brood development stage		Nonacs and Carlin 1990
		<i>Formica exsecta</i> ^(L)	Depends on queen number		Sundström et al. 1996
		<i>Linepithema humile</i> ^(L)	Depends on queen presence, brood development stage		Aron et al. 1994; Passera et al. 1995; Passera and Aron 1996
<i>Monomorium pharaonis</i> ^(L)	Depends on brood development stage		Peacock et al. 1954; Warner et al. 2016		

Table 1 (continued)

Discrimination context	Development stage	Species	Evidence for discrimination	Recognition cues used	References
Trophic vs. viable	Egg	<i>Lasius niger</i> (larva)	Yes		Baroni Urbani 1991
		<i>Novomessor cockerelli</i>	Yes		Hölldobler and Carlin 1989
		<i>Rhytidoponera sp.12</i>	Yes		Tay and Crozier 2000
		<i>Messor semirufus</i> (larva)	No		Baroni Urbani 1991
		<i>Myrmecia gulosa</i>	Depends on worker size	Egg odor	Dietemann 2002; Dietemann et al. 2005
Worker-destined vs. queen-destined	Larva, pupa	<i>Harpegnathos saltator</i> ^(L)	Yes	Larva odor	Penick and Liebig 2017
		<i>Aphaenogaster senilis</i> ^(L)	Depends on queen presence		Villalta et al. 2016
		<i>Linepithema humile</i> ^(L)	Depends on queen presence		Passera et al. 1995; Klobuchar and Deslippe 2002
		<i>Monomorium pharaonis</i> ^(L)	Depends on queen presence, brood development stage	Larval pilosity	Edwards 1991; Warner et al. 2016
		<i>Myrmica rubra</i> ^(L,P)	Depends on queen presence	Larval secretions	Brian 1973c, b, 1975a
		<i>Solenopsis invicta</i> ^(L)	Depends on queen presence, brood development stage		Glancey et al. 1970; Vargo and Fletcher 1986; Klobuchar and Deslippe 2002
Size, age	Young vs. old larva	<i>Monomorium pharaonis</i>	Yes		Walsh et al. 2018b
	Larva vs. pupa; small larva vs. large larva, egg vs. larva	<i>Lasius niger</i>	Yes		Lenoir 1981
	4 th instar larva vs. other larval instars	<i>Solenopsis invicta</i>	Yes		Petralia and Vinson 1979b
	Larva vs. pupa	<i>Acromyrmex echinator</i>	Yes		Fouks et al. 2011
		<i>Myrmica rubra</i>	Yes		Brian 1975a
		<i>Myrmica sabuleti</i>	Yes		Thomas et al. 2013
		<i>Myrmica scabrinodis</i>	Yes		Casacci et al. 2013
		<i>Myrmica schenki</i>	Yes		Thomas et al. 1998
		<i>Solenopsis invicta</i>	Yes	Larva odor, pupa odor	Glancey et al. 1970
	Larva vs. pupa, small vs. large larva	<i>Linepithema humile</i>	Depends on queen presence		Passera et al. 1995

Discrimination abilities of workers were tested unless otherwise noted in parentheses behind the species name. For discrimination contexts in which more than one development stage was tested, details on the tested stage are given in superscript behind the species name (*E* egg, *L* larva, *P* pupa, ? unknown). Where available, information on the cues used for recognition is given

Wheeler (1910, 1918) first proposed that ant larvae emit chemical attractants. Worker attraction towards conspecific brood odors was then demonstrated in the army ants *Neivamyrmex opacithorax* and *Eciton* spp. (Watkins and Cole 1966; Schneirla 1971) and shortly after confirmed in *Atta cephalotes* (Robinson and Cherrett 1974), *Myrmica rubra* (Brian 1975a), and *Solenopsis invicta* (Glancey et al.

1970, but see Walsh and Tschinkel 1974). These findings, together with the fact that ant workers are known to readily accept and rear conspecific non-nestmate brood (Table 2) inspired researchers to search for ant brood pheromones, i.e., chemical substances emitted by immature individuals that elicit a specific response in conspecific adults (Morel and Vander Meer 1988; Vander Meer and Alonso 1998).

Table 2 Overview of studies conducted on ant brood recognition and discrimination in the context of conspecific interactions

Discrimination context	Development stage	Species	Evidence for discrimination	Recognition cues used	References
Nestmate vs. non-nestmate	Egg, larva, pupa	<i>Acromyrmex subterraneus subterraneus</i> ^(L,P)	Yes	Pupa odor	Viana et al. 2001
		<i>Atta sexdens rubropilosa</i> ^(E,L,P)	Yes		Araujo et al. 1996
		<i>Leptothorax acervorum</i> (queen) ^(E)	Yes		Bourke 1994
		<i>Leptothorax longispinosus</i> ^(L)	Yes	Larva odor	Hare 1996; Swan and Hare 2012
		<i>Myrmica schencki</i> ^(L)	Yes	Larva odor	Akino et al. 1999
		<i>Temnothorax nylanderii</i> ^(L)	Yes		Swan and Hare 2012
		<i>Temnothorax parvulus</i> ^(L)	Yes		Swan and Hare 2012
		<i>Acromyrmex laticeps nigrosetosus</i> ^(L,P)	No		Souza et al. 2006
		<i>Formica aquilonia</i> (larva) ^(E)	No		Schultner et al. 2013
		<i>Formica gnava</i> ^(P)	No		Goodloe and Topoff 1987
		<i>Formica paralugubris</i> ^(P)	No		Maeder et al. 2005
		<i>Formica pratensis</i> ^(P)	No		Rosengren and Cherix 1981
		<i>Formica sanguinea</i> ^(P)	No		Mori et al. 1992
		<i>Formica schaufussi</i> ^(P)	No		Goodloe and Topoff 1987
		<i>Messor semirufus</i> (larva) ^(E)	No		Baroni Urbani 1991
		<i>Myrmecia sp.</i> ^(E,L,P)	No		Haskins and Haskins 1950
		<i>Oecophylla smaragdina</i> ^(L)	No		Krag et al. 2010
		<i>Rhytidoponera confusa</i> ^(L)	No		Crosland 1988
		<i>Promyrmecia sp.</i> ^(E,L,P)	No		Haskins and Haskins 1950
		<i>Tapinoma erraticum</i> ^(P)	No		Meudec 1978
		<i>Acromyrmex echinator</i> ^(L,P)	Depends on worker caste		Fouks et al. 2011; Larsen et al. 2014
		<i>Atta cephalotes</i> ^(L,P)	Depends on brood development stage		Robinson and Cherrett 1974
		<i>Camponotus floridanus</i> ^(P)	Depends on brood sex		Carlin and Schwartz 1989; Nonacs and Carlin 1990
		<i>Cataglyphis cursor</i> ^(L)	Depends on worker pre-eclosion experience		Lenoir 1984; Isingrini et al. 1985; Isingrini 1987; Isingrini and Lenoir 1988
<i>Dinoponera quadricaps</i> ^(E)	Depends on worker age		Tannure-Nascimento et al. 2009		
<i>Ectatomma tuberculatum</i> ^(L)	Depends on worker age		Fénéron and Jaisson 1995		

Table 2 (continued)

Discrimination context	Development stage	Species	Evidence for discrimination	Recognition cues used	References
		<i>Formica fusca</i> (+ larva) ^(E,P)	Depends on queen presence, worker post-eclosion experience		Jaisson 1975; Helanterä and Sundström 2007; Helanterä et al. 2007, 2014; Helanterä and Ratnieks 2009a; Pulliainen et al. 2019
		<i>Formica exsecta</i> ^(P)	Depends on brood caste		Pulliainen et al. 2018
		<i>Formica lugubris</i> ^(P)	Depends on brood origin		Rosengren and Cherix 1981; Rosengren et al. 1994; Maeder et al. 2005
		<i>Formica rufa</i> ^(P)	Depends on worker post-eclosion experience, brood origin		Le Moli and Passetti 1977, 1978; Rosengren and Cherix 1981
		<i>Formica selysi</i> ^(E)	Depends on worker origin		Meunier et al. 2010
		<i>Lasius niger</i> (larva) ^(E,L,P)	Depends on identity of discriminator		Lenoir 1981; Baroni Urbani 1991
		<i>Myrmica rubra</i> ^(L)	Depends on experimental setup		Elmes and Wardlaw 1983; Solazzo et al. 2013
		<i>Temnothorax ambiguus</i> ^(L)	Depends on brood origin		Swan and Hare 2012
		<i>Temnothorax unifasciatus</i> ^(P)	Depends on enslavement status of colony		Delattre et al. 2012
Monogyne colony vs. polygyne colony	Egg	<i>Formica selysi</i>	Yes	Egg odor	Meunier et al. 2011

Discrimination abilities of workers were tested unless otherwise noted in parentheses behind the species name. For discrimination contexts in which more than one development stage was tested, details on the tested stage are given in superscript behind the species name (*E* egg, *L* larva, *P* pupa, ? unknown). Where available, information on the cues used for recognition is given

Such brood pheromones exist in the honey bee *Apis mellifera* (Le Conte et al. 1990), where they are produced in larval salivary glands (Le Conte et al. 2006) and have a distinct role in modulating worker behavior and physiology (Mohammedi et al. 1996; Le Conte et al. 2001).

A first attempt at characterizing ant brood pheromones was conducted by Bigley and Vinson (1975), who identified the pupal pheromone of *Solenopsis invicta* as *triolein*. Similarly, Glancey and Dickens (1988) claimed to have isolated a larval brood pheromone from the same species. However, these identifications were later claimed to be inaccurate (Vander Meer 1983), and the overall existence of ant brood pheromones argued against, with particular focus on the unreliability of the performed assays and the lack of species specificity in the action of the identified compounds (Morel and Vander Meer 1988; Vander Meer and Morel 1988; Vander Meer and Alonso 1998). Indeed, interspecific brood adoption by worker ants has been widely reported (Table 3), lending support to the notion that ant

brood pheromones—by definition, substances that elicit reactions from conspecifics—do not exist. Careful work on brood odors in the fire ant *S. invicta* (reviewed in Tschinkel 2006), as well as recent studies on a number of different species spanning the ant phylogeny have demonstrated that the presence of brood influences adult behavior and reproductive physiology (Heinze et al. 1996; Endler et al. 2004; Teso et al. 2013; Ebie et al. 2015; Ulrich et al. 2016; Chandra et al. 2018), and that this inhibition can be caused by larval contact odors alone (Villalta et al. 2015). While these results seemingly provide support for the idea that ant brood pheromones exist, studies testing whether such brood odors act in a species-specific manner are still lacking. One can hope that a species-comparative approach using modern methods of chemical analysis and carefully designed bioassays will help elucidate the chemical nature of these compounds in the future.

Beyond this burst of interest in brood pheromones, individual brood items, in particular larvae, were often regarded

Table 3 Overview of studies conducted on ant brood recognition and discrimination in the context of hetero-specific interactions

Discrimination context	Development stage	Species	Evidence for discrimination	Recognition cues used	References
Conspecific vs. hetero-specific	Egg, larva, pupa	<i>Acromyrmex octospinosus</i> ^(L)	Yes	Larva odor	Febvay et al. 1984
		<i>Acromyrmex subterraneus subterraneus</i> ^(L,P)	Yes	Larva odor, pupa odor	Viana et al. 2001
		(H) <i>Formica lemaitrei</i> ^(E)	Yes		Chernenko et al. 2011
		<i>Formica neogagates</i> ^(P)	Yes		Zimmerli and Mori 1993
		<i>Formica paratugubris</i> ^(P)	Yes		Maeder et al. 2005
		(SP) <i>Formica pratensis</i> ^(P)	Yes		Rosengren and Cherix 1981
		(H) <i>Formica schaufussii</i> ^(P)	Yes		Goodloe and Topoff 1987
		(H) <i>Leptothorax muscorum</i> ^(L,P)	Yes		Schumann and Buschinger 1991
		<i>Myrmica rubra</i> ^(L)	Yes		Brian 1975a
		<i>Myrmica sabuleti</i> ^(L)	Yes		Elmes and Wardlaw 1983
		<i>Myrmica schenckii</i> ^(P)	Yes		Akino et al. 1999
		(BT) <i>Polyrhachis lama</i> ^(E,L,P)	Yes		Witte et al. 2009
		(H) <i>Formica gnava</i> ^(E)	No		Johnson et al. 2005
		(SP) <i>Formica sanguinea</i> ^(P)	No		Mori et al. 1992
		<i>Lasius niger</i> ^(L,P)	No		Akino and Yamaoka 1998
		<i>Lasius sakagami</i> ^(L,P)	No		Akino and Yamaoka 1998
		(H) <i>Leptothorax acervorum</i> ^(P)	No		Schumann and Buschinger 1991
		<i>Myrmica laevinodis</i> ^(L)	No		Plateaux 1960b
		<i>Myrmica ruginodis macrogyna</i> ^(L)	No		Elmes and Wardlaw 1983
		<i>Myrmica scabrinodis</i> ^(L)	No		Elmes and Wardlaw 1983
(H) <i>Rhytidoponera calybaea</i> ^(L)	No		Crosland 1988		
(H) <i>Rhytidoponera confusa</i> ^(L)	No		Crosland 1988		
(BT) <i>Solenopsis fugax</i> ^(L)	No		Plateaux 1960c		
(H) <i>Tetramorium caespitum</i> ^(L)	No		Plateaux 1960c		

Table 3 (continued)

Discrimination context	Development stage	Species	Evidence for discrimination	Recognition cues used	References
		(H) <i>Temnothorax unifasciatus</i> ^(P)	No		Delattre et al. 2012
		<i>Camponotus abdominalis</i> ^(L)	Depends on identity of intruder, worker age		Errard 1984
		<i>Camponotus floridanus</i> ^(P)	Depends on worker post-eclosion experience, worker age		Carlin et al. 1987
		<i>Camponotus senex</i> ^(L)	Depends on identity of intruder, worker age		Errard 1984
		<i>Camponotus tortuganus</i> ^(P)	Depends on worker post-eclosion experience, worker age		Carlin et al. 1987
		(H) <i>Diacamma sp.</i> ^(E,L,P)	Depends on presence of social parasite		Witte et al. 2009
		(H) <i>Formica cunicularia</i> ^(P)	Depends on identity of intruder	Pupa odor, pupa size	Mori and Le Moli 1988; Mori et al. 1996
		(H) <i>Formica fusca</i> ^(E,P)	Depends on presence of social parasite, identity of intruder, worker post-eclosion experience		Jaisson 1975; Chernenko et al. 2011, 2013
		(SP) <i>Formica rufa</i> ^(P)	Depends on identity of intruder, worker post-eclosion experience	Pupa odor	Le Moli and Passetti 1977, 1978; Le Moli 1978; Rosengren and Cherix 1981; Maeder et al. 2005
		(SP) <i>Formica lugubris</i> ^(P)	Depends on identity of intruder, worker post-eclosion experience		Rosengren and Cherix 1981; Le Moli and Mori 1982; Rosengren et al. 1994; Mori et al. 1996; Maeder et al. 2005
		(H) <i>Formica occulta</i> ^(E,P)	Depends on identity of intruder		Zimmerli and Mori 1993; Johnson et al. 2005
		(SP) <i>Formica polyctena</i> ^(P)	Depends on identity of intruder, presence of social parasite, worker post-eclosion experience		Jaisson 1975; Jaisson and Fresneau 1978; Rosengren and Cherix 1981
		(H) <i>Formica rufibarbis</i> ^(P)	Depends on identity of intruder		Mori et al. 1996
		(SP) <i>Formicoxenus provancheri</i> ^(L)	Depends on worker post-eclosion experience		Errard et al. 1992
		(H) <i>Myrmica incompleta</i> ^(L)	Depends on worker post-eclosion experience		Errard et al. 1992
		<i>Tapinoma erraticum</i> ^(P)	Depends on identity of intruder, presence of conspecific brood		Meudec 1978
		(H) <i>Temnothorax ambiguus</i> ^(L)	Depends on worker pre-eclosion experience, worker post-eclosion experience		Hare and Alloway 1987; Linksvayer 2007; Swan and Hare 2012
		(H) <i>Temnothorax curvispinosus</i> ^(L,P)	Depends on identity of intruder, development stage of intruder, sex of intruder, caste of intruder, geographical origin of intruder, presence of social parasite		Linksvayer 2007; Achenbach and Foitzik 2009; Achenbach et al. 2010

Table 3 (continued)

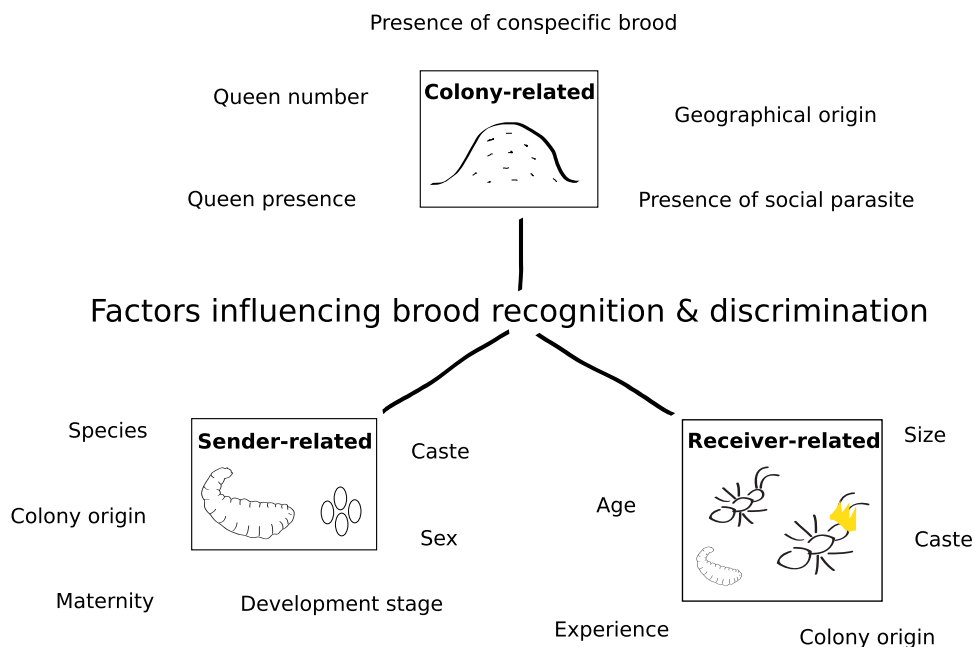
Discrimination context	Development stage	Species	Evidence for discrimination	Recognition cues used	References
		(H) <i>Temnothorax longispinosus</i> ^(L,P)	Depends on identity of intruder, development stage of intruder, sex of intruder, caste of intruder, geographical origin of intruder, presence of social parasite, worker pre-eclosion experience, worker post-eclosion experience		Hare and Alloway 1987; Alloway and Hare 1989; Hare 1996; Linksvayer 2007; Achenbach and Foitzik 2009; Achenbach et al. 2010; Swan and Hare 2012
		<i>Temnothorax nylander</i> ^(L)	Depends on presence of conspecific brood		Plateaux 1960a

Discrimination abilities of workers were tested unless otherwise noted in parentheses behind the species name. For discrimination contexts in which more than one development stage was tested, details on the tested stage are given in superscript behind the species name (*E* egg, *L* larva, *P* pupa, ? unknown). Where available, information on the cues used for recognition is given. Species are denoted as hosts (H), social parasites (SP) or brood thieves (BT) if information on species ecology was available

as chemically insignificant. Brood hydrocarbon profiles have indeed been shown to be less complex than adult cuticular profiles in some species (Viana et al. 2001; Richard et al. 2007; Fouks et al. 2011). However, the complexity of egg, larval and pupal profiles can also mirror that of adult profiles (Bagnères and Morgan 1991; Akino et al. 1999; Elmes et al. 2002; Souza et al. 2006; Tannure-Nascimento et al. 2009; Helanterä and d'Ettoire 2014). We now know that brood surface chemistry can be species, population, and colony-specific (Brian 1975a; Le Moli and Passetti 1978; Mori and Le Moli 1988; Hare 1996; Akino et al. 1999; Viana et al. 2001; Johnson et al. 2005; Souza et al. 2006; Richard et al. 2007; Achenbach and Foitzik 2009; Achenbach et al. 2010; Schultner et al. 2013; Helanterä and d'Ettoire 2014; Pulliainen et al. 2018, Peignier et al. 2019), and contain information about traits like viability (Dietemann et al. 2005), maternity (Monnin and Peeters 1997; Endler et al. 2004, 2006; d'Ettoire et al. 2004, 2006; Dietemann et al. 2005; Meunier et al. 2010; Shimoji et al. 2012; Helanterä and d'Ettoire 2014), development stage (Johnson et al. 2005; Richard et al. 2007), sex (Achenbach et al. 2010), caste (Brian 1975a; Achenbach et al. 2010; Penick and Liebigh 2017), and colony social structure (Meunier et al. 2011).

Brood recognition can also be based on non-chemical cues such as morphology, behavior, and acoustic signals. Ant larvae show striking diversity in body size and shape, overall mobility, and morphology of body hairs (Wheeler 1918; Wheeler and Wheeler 1953, 1976, 1986). In particular the size, shape, distribution and density (= pilosity) of larval hairs can differ between species, as well as between developmental stages, sexes and castes within single species (Petralia and Vinson 1978, 1979a; Solis et al. 2010b, a, 2011, 2012b, a; Fox et al. 2011; Penick et al. 2012; Wang et al. 2017). In *Monomorium* and *Solenopsis* ants, differences in the pilosity of worker- and queen-destined larvae may help workers recognize the two castes (Edwards 1991; Fox et al. 2011). In *Myrmica* ants, the increasing pilosity of larvae over the course of development has been suggested to be crucial for recognition, together with brood chemistry and tactile cues such as turgidity, size, shape, and cuticle surface properties (Brian 1975a). *Formica cunicularia* workers also seem to use a combination of cues to recognize brood as only heterospecific brood that resembles conspecific brood in both size and odor are accepted (Mori and Le Moli 1988). Larval behavior can also transmit information to workers, for instance in the context of nutritional provisioning. This is exemplified by the correlation between larval head movements and worker feeding behavior in *Myrmica rubra* (Creemers et al. 2003). The pupae of the closely related species *Myrmica scabrinodis* communicate acoustically with workers using stridulatory organs (Casacci et al. 2013). Judging from the sheer diversity of ant brood morphology, there are many more such fascinating traits to be discovered.

Fig. 1 Overview of factors influencing brood recognition and discrimination in ants



Ontogeny of brood recognition and discrimination behavior

Ant workers develop from female eggs, which hatch into larvae that pass through 3–5 instars (depending on the species) and a short pre-pupal phase, before undergoing complete metamorphosis and remaining in a pupal stage until eclosing as adults. Adult ants detect chemical compounds with a chemosensory system, including a range of proteins in the antennal sensilla that detect, bind and carry odorant molecules (Ozaki et al. 2005; Kulmuni and Havukainen 2013; McKenzie et al. 2014; Pask et al. 2017; Slone et al. 2017; McKenzie and Kronauer 2018). The olfactory stimuli are then perceived in the antennal lobes and the higher integration centres in the brain, and ultimately lead to behavioral responses (Ozaki and Wada-Katsumata 2010; Tribble et al. 2017; Yan et al. 2017). Social interactions play a key role in modulating neurophysiological processes, and lack thereof can inhibit growth and development of important learning and memory centers in the brain, in addition to other negative neurochemical effects (Boulay et al. 2000; Wada-Katsumata et al. 2011; Seid and Junge 2016).

Although the neurophysiology of brood recognition has not been studied, current data suggest that odor-based recognition abilities of worker ants are shaped by the integration of multiple chemical templates during both larval and adult life. For example, *Cataglyphis cursor* workers are able to discriminate larvae according to colony origin within 24 h of eclosion (Isingrini and Lenoir 1988), indicating that pre-imaginal learning shapes recognition abilities (Isingrini et al. 1985). Similarly, pre-imaginal learning appears to affect recognition abilities in *Camponotus* spp., *Aphaenogaster senilis*

and *Leptothorax* spp. workers (Hare and Alloway 1987; Carlin and Schwartz 1989; Signorotti et al. 2014). While this suggests that this phenomenon is universal in ants, there are also examples, where pre-eclosion experience does not affect discriminatory behavior, e.g., in *Temnothorax parvulus* (Blatrix and Sermage 2005).

After eclosing as adults, young workers typically act as nurses within the nest, before transitioning to become foragers when they are older (but see Muscedere et al. 2009). This age-based division of labor can be reflected in both recognition abilities and discriminatory behavior. In *Ectatomma tuberculatum*, only 2–10 week old workers (the age that corresponds to the nursing period in this species) discriminate between nestmate and non-nestmate larvae and pupae, whereas older workers lose the preference for nestmate brood (Fénéron and Jaisson 1992, 1995). Similarly, in *Dinoponera quadricaps* only 1–6 week old workers (i.e., nurses) were able to discriminate between nestmate and non-nestmate eggs, whereas younger (callows) or older (foragers) workers were not (Tannure-Nascimento et al. 2009). The change in recognition capacity seems to be related to the current task of the worker, rather than to age per se (Fénéron and Jaisson 1992), and the loss of preference for nestmate eggs in foragers might result from a lack of continuous updating of the chemical template (Fénéron and Jaisson 1995). This is supported by studies showing that workers adopt unfamiliar brood more readily if they do not have access to a chemical template of familiar brood or if they have been previously exposed to unfamiliar con- or heterospecific brood (Jaisson 1975; Le Moli and Passetti 1977; Jaisson and Fresneau 1978; Le Moli and Passetti 1978; Lenoir 1981; Le Moli and Mori 1982; Isingrini et al. 1985; Carlin et al. 1987; Hare and

Alloway 1987; Helanterä et al. 2007; Helanterä and Ratnieks 2009a; Swan and Hare 2012). For example, *F. fusca* workers taken from a colony enslaved by *Formica sanguinea* accept foreign brood, while workers taken from unparasitized nests do not (Jaisson 1975).

Some ant species have morphological worker castes that are specialized for discrete tasks; such morphological specialization may also influence recognition and discrimination abilities. In *Acromyrmex echinator*, different morphological castes differ in their aggression towards conspecifics (Larsen et al. 2014). Compared to minor workers, major workers are more aggressive towards adult conspecifics and discriminate against non-nestmate brood. This is thought to be the result of lower sensitivity to nestmate odors in minor workers, which usually do not defend the nest against intruders. Even in species without morphological worker castes, workers can vary in size, and this may affect task partitioning and consequently, brood-discrimination behavior. In colonies of *Myrmecia gulosa* ants, small workers kill viable eggs while large workers do not (Dietemann 2002). Whether this is due to differences in recognition abilities or experience, or because large workers simply refrain from egg killing, is not known.

Overall, although recognition mechanisms in ants have not been studied exhaustively, it is known that they are highly flexible, context-dependent and modulated by dynamic thresholds and integration of multiple templates (Gamboa et al. 1991; van Zweden and d'Ettorre 2010; Newey 2011; Sturgis and Gordon 2012). While we are beginning to understand how adult ants perceive social information (Ozaki et al. 2005; Brandstaetter et al. 2011; Pask et al. 2017; Tribble et al. 2017; Yan et al. 2017; Neupert et al. 2018), comparative analyses across species and genera are needed to draw general conclusions about the ability of workers to recognize brood, and how such abilities may be ontogenetically constrained.

Brood recognition: why?

Given that brood from conspecific and even heterospecific nests are often readily accepted (Tables 2, 3), it may appear as if brood discrimination has no selective advantage. Indeed, as the immature stages of ants are largely immobile, they are not potential intruders of colonies. Compared to discrimination of adult individuals, the ability to recognize and discriminate brood may thus be under less stringent selection, and general cues identifying brood as brood may override more specific information on individual traits (Carlin 1988). Nonetheless, there are several scenarios in which precise brood recognition and discrimination are predicted to evolve. First, the identity of brood (e.g., developmental stage, sex, caste, maternity) can be a key modulator

of within-colony interactions, particularly in the case of colony-level conflicts over resource allocation (Schultner et al. 2017). Second, recognition of, and discrimination against, foreign brood may be crucial in maintaining colony integrity, especially in species which are targeted by social parasites that exploit the brood care behavior of the host (Schmid-Hempel 1995). In the second section of this review, we discuss the adaptive value of accurate brood recognition and discrimination and review the evidence for discrimination on three organizational levels (within nests, between conspecifics, and between species) across the ant phylogeny.

Within-nest interactions

Within ant nests, the needs of brood play a major role in dictating the behavior and physiology of adult nestmates (Schultner et al. 2017). For example, since ant brood are not restricted to individual cells but instead reared in piles, nurse workers continually adjust the location of brood within nests to ensure optimal microclimatic conditions for growth and development (Brian 1973a; Hölldobler and Wilson 1990; Penick and Tschinkel 2008; Römer and Roces 2014). As the needs of brood can vary depending on traits like developmental stage, sex and caste, workers are under selection to recognize brood precisely to adjust rearing conditions on an individual basis. Some ants are known to sort brood according to developmental stage or size (Le Masne 1953; Sendova-Franks et al. 2004), which can help increase efficiency of brood care (Franks and Sendova-Franks 1992) and prevent within-brood cannibalism (Rüger et al. 2007). From an inclusive fitness-centered point of view, discriminating developing individuals according to traits like maternity, sex, and caste can play a key role in within-colony conflicts over reproductive dominance, sex allocation and caste allocation (Schultner et al. 2017).

Feeding interactions

A colony's feeding interactions are centered around larvae, which are both the major consumers of worker provisions and providers of the fundamental service of protein processing to the colony (Hölldobler and Wilson 1990). Access to information about brood traits such as developmental stage, size, sex, maternity, caste and hunger level can help workers optimize their feeding behavior, for example in cases, where brood of different ages, sexes, or castes have different nutritional requirements (Brian 1981; Boomsma and Isaaks 1985; Cassill and Tschinkel 1996; Smith et al. 2008b; Smith and Suarez 2010). Recognizing hungry larvae can help workers optimally allocate food (Brian and Abbott 1977; Cassill and Tschinkel 1999; Lopes et al. 2005) and both behavioral and chemical cues have been implicated in larval begging (Le Masne 1953; Vowles 1955; Cassill and Tschinkel

1995; Creemers et al. 2003; Kaptein et al. 2005; Pegnier et al. 2019). Importantly, since it is commonly assumed that queen-worker caste differentiation is modulated by differences in individual nutritional provisioning, workers should be able to adjust their feeding behavior according to larval caste to produce the polymodal size distribution of female castes observed in many species (Trible and Kronauer 2017).

Information about brood traits may also be useful in the context of brood cannibalism, i.e., when adult colony members consume brood, feed brood to larvae during periods of resource shortage (Crespi 1992), or when larvae selfishly consume other brood (Baroni Urbani 1991; R uger et al. 2007; Schultner et al. 2013, 2014). According to inclusive fitness theory, least related brood should be consumed first, along with early brood stages that have not yet consumed large amounts of colony resources (Elgar and Crespi 1992). Prerequisites for such discriminatory behavior are the ability to assess the relatedness or developmental stage of brood. This appears to be the case in *Formica* wood ants, in which larvae preferentially cannibalize unrelated eggs (Schultner et al. 2013, 2014). Furthermore, it may be important to discriminate between viable and unviable eggs, particularly in species that produce trophic eggs that are meant to be consumed (e.g., Dietemann and Peeters 2000). This is the case in *Myrmecia gulosa*, where workers destroy unviable but not viable worker-laid eggs (Dietemann et al. 2005). In the ant *Lasius niger*, larvae discriminate between viable and trophic eggs and consume the latter preferentially (Baroni Urbani 1991). In contrast, *Leptothorax acervorum* queens do not discriminate between viable and trophic eggs and consume both at similar rates (Bourke 1991).

Maternity and kinship

In many species, workers are able to lay unfertilized, male-destined eggs (H lldobler and Wilson 1990; Bourke and Franks 1995a). Worker reproduction decreases colony productivity and efficiency (e.g., Hartmann et al. 2003). As a result, reproducing workers are often punished by nestmate queens or workers, either via direct aggression or destruction of worker-laid eggs (policing; Ratnieks 1988). This is most likely mediated by queen-borne fertility signals on the egg surface (Holman et al. 2010), which appear to be conserved across social Hymenoptera (Van Oystaeyen et al. 2014). Indeed, discrimination between queen and worker-laid eggs has been demonstrated in a number of species and is often linked to differences in the odor profiles of eggs (Table 1). In the carpenter ant *Camponotus floridanus*, chemical cues can even distinguish eggs laid by highly fertile queens from those laid by queens of low fertility (Endler et al. 2006). Whether workers act on the information provided by egg odor profiles can depend on the presence of the queen

(d’Ettorre et al. 2004; Helanter  and Sundstr m 2007) and colony origin (van Zweden et al. 2009b).

In colonies with more than one reproductive individual (i.e., multiple queen colonies, colonies with totipotent workers), brood cues can help signal reproductive dominance. For example, in queenless *Dinoponera* and *Diacamma* ants, societies consist of morphologically similar, totipotent individuals that can produce both male and female eggs. Here, reproductive dominance is established via behavioral interactions, and eggs laid by subordinate individuals are preferentially destroyed; this behavior is most likely mediated by differences in the proportions of certain hydrocarbons on the egg surface (Monnin and Peeters 1997; Shimoji et al. 2012).

Finally, in colonies that contain more than one reproducing queen, workers can increase their inclusive fitness by selectively directing their altruistic actions towards their closest relatives (so-called nepotism). Overall, nepotism in social insects is rare (Boomsma and d’Ettorre 2013), but Hannonen and Sundstr m (2003) found that *Formica fusca* workers were able to assess the kinship of eggs in their care and act on this information by favouring eggs of a more closely related queen. Holzer et al. (2006) attempted to confirm these results by presenting *Formica exsecta* workers with a choice between sisters and unrelated eggs but failed to find signs of nepotism. Instead, they concluded that the distinctive pattern of brood composition was caused by differential egg viability, casting doubt on the earlier study. Nevertheless, a study on egg signature mixtures in *Formica* ants showed that egg chemical profiles are highly variable and potentially provide sufficient information for discrimination between matriline within nests (Helanter  and d’Ettorre 2014). Whether or not this information is used likely depends on species-specific biology: in contrast to *F. exsecta*, *F. fusca* is a common host to ant social parasites and displays excellent discrimination abilities (Helanter  and Sundstr m 2007; Helanter  and Ratnieks 2009a; Chernenko et al. 2011, 2013; Helanter  et al. 2011; Martin et al. 2011; Pulliainen et al. 2019). Contrasting patterns of brood discrimination in different species may thus be linked to differential selection pressures.

Sex allocation

Ants, like all Hymenoptera, are haplodiploid, meaning that unfertilized, haploid eggs give rise to males, whereas fertilized, diploid eggs give rise to females. This mode of sex determination results in relatedness asymmetries between a singly mated mother queen and her male and female offspring: while the queen is equally related to offspring of both sexes (relatedness coefficient $r = 0.5$), female offspring are, on average, more closely related to each other ($r = 0.75$) than they are to their brothers ($r = 0.25$). Relatedness asymmetries resulting from

haplodiploidy can cause conflict to arise between queens and workers over the sex of brood. In colonies with a single, singly inseminated queen, workers prefer investing more in female production (specifically production of new queens, so-called gynes), while the queen prefers equal investment in both sexes (Trivers and Hare 1976). Whether an egg is fertilized is thought to be under the direct control of the queen herself (Ratnieks and Keller 1998), allowing her to modulate the primary sex ratio of brood (Passera et al. 2001; Rosset and Chapuisat 2006). However, workers can attempt to bias secondary sex ratios, i.e., investment towards gynes, by destroying male brood or biasing caste fate of diploid brood (Helanterä and Ratnieks 2009b). In species where workers have retained the ability to produce haploid eggs, they may also attempt to replace the queen's sons with their own (Wenseleers and Ratnieks 2006).

For adults to be able to selectively destroy male brood or preferentially rear gynes, they must be able to discriminate between male and female brood (Nonacs and Carlin 1990). A number of studies have approached this question by comparing the primary and secondary sex ratios produced by natural colonies and inferring selective removal of males (Brian 1981; Nonacs and Carlin 1990; Edwards 1991; Passera et al. 1995; Aron et al. 1995; Jemielity and Keller 2003; Rosset and Chapuisat 2006; Warner et al. 2016). However, although it is clear that workers can discriminate between sexes, and that this behavior depends on factors such as brood developmental stage, queen presence and queen number (Table 1), next to nothing is known about the cues involved. Sex-specific recognition cues are probably not directly linked to the ploidy state of eggs, since queen-laid male eggs would otherwise be destroyed in the process. In line with this, *F. selysi* workers are able to discriminate haploid worker-laid eggs from haploid queen-laid eggs, probably with the help of queen-derived odors on the egg surface (Meunier et al. 2010). As the sex allocation preferences of queens and workers vary with colony kin structure (Bourke and Franks 1995b), this should also influence whether brood are under selection to mask or signal sex (Nonacs and Carlin 1990; Schultner et al. 2017). In the past, comparisons of sex-specific brood traits, and in particular brood odor profiles, were hindered by the lack of appropriate methods with which researchers themselves could differentiate between the sexes. Fortunately, a recent study describing differences in male and female genital disc morphology in larvae has taken a first step towards overcoming this hurdle (Penick et al. 2014). In the future, systematic studies of sex-specific brood traits across different kin structures will help us understand the causes and constraints of brood discrimination according to sex.

Caste allocation

Adult queens and workers differ in their relatedness to developing females because of haplodiploidy; this relatedness asymmetry can cause them to exhibit differing fitness interests regarding allocation of resources toward new queens (Beekman and Ratnieks 2003; Ratnieks et al. 2006). In addition, female larvae are predicted to be under selection to increase their chances of developing into a queen rather than a worker, since a female is more closely related to her own offspring than to offspring of other developing individuals (Bourke and Ratnieks 1999; Dobata 2012). In ants, caste determination factors are manifold and range from intrinsic traits such as genotype (Helms Cahan and Keller 2003) to social environmental factors such as worker behavior (Penick and Liebig 2012). In species with genetic caste determination, caste differences should manifest early on in development and information on caste should, in principle, be available to rearing workers throughout the course of development. In species with environmental caste determination, differences are predicted to manifest sometime during larval development or during pupation. As queens are larger than workers in most species, the trait most commonly associated with queen caste during development is body size (Trible and Kronauer 2017). Accordingly, in the fire ant *Solenopsis invicta* larval body size correlates with the rate, but not duration, of trophallaxis between workers and larvae (Cassill and Tschinkel 1995, 1999). In contrast, larval size had no effect on worker brood care behavior in the ant *Myrmica rubra* (Brian 1975b). Because of limited knowledge on the timing of caste determination across the ant phylogeny, only a handful of studies have attempted to find morphological, physiological or chemical traits associated with female caste. Nevertheless, there is sufficient evidence showing that workers adjust their behavior according to the caste of female brood (Table 1). Brian (1975a) for example found that queen-potential *Myrmica* larvae secrete oily droplets, and that workers preferentially fed secreting larvae; as a result, secreting larvae more often developed into queens. In the presence of an adult queen; however, queen-potential larvae were repeatedly attacked and bitten, causing them to develop into workers (Brian 1970, 1973b). A similar phenomenon was observed in the ant *Harpegnathos saltator*, in which queen and worker-destined larvae differ in their hydrocarbon profiles and workers preferentially bite queen-destined larvae in the presence of an adult queen (Penick and Liebig 2017). In queen-right *Linepithema humile* colonies, queen-destined larvae are also killed selectively, while queen-destined pupae, worker brood and male brood are spared (Passera et al. 1995). Worker behavior towards worker- and

queen-destined larvae also differs in *Aphaenogaster gracilis*, even though the hydrocarbon profiles of the two castes are highly similar (Villalta et al. 2016). Thus, while there is little doubt that workers can differentiate brood according to caste, and that this ability is not phylogenetically constrained, more studies are needed to draw conclusions about the cues involved.

Interactions with conspecifics

In the context of conspecific interactions, accepting non-nestmate worker brood can be beneficial, since workers can successfully integrate into an adoptive colony, without the resources needed to rear them. In fact, in some species conspecific brood theft is a common strategy to increase growth and ensure survival of incipient colonies (Pollock and Rissing 1989; Paul et al. 2016). In contrast, non-nestmate sexual brood should not be accepted indiscriminately, since male- and queen-destined individuals may use colony resources without contributing to colony fitness. Concordantly, in the ant *Formica exsecta*, workers retrieve both nestmate and non-nestmate worker pupae at similar rates but prefer nestmate sexual pupae to non-nestmates (Pulliainen et al. 2018). These results highlight why discrimination against non-nestmate brood can be beneficial in some contexts but not in others and may help explain the broad range of results reported by studies on conspecific brood discrimination. For example, workers of the ant *Formica fusca* discriminate between nestmate and non-nestmate eggs only when an adult queen is present in the colony (Helanterä and Sundström 2007) and when they have been exposed to nestmate eggs during the first few days of adult life (Helanterä et al. 2007; Helanterä and Ratnieks 2009a). Removal of the queen and exposure to alien eggs during the sensitive period strongly reduce discrimination between nestmate and non-nestmate brood. In contrast, workers of the closely related species *Formica gnava* do not seem to discriminate between nestmate and non-nestmate pupae, even when the queen is present (Goodloe and Topoff 1987). Such differential responses may be explained by development stage-specific responses or species-specific ecologies. One explanation for precise discrimination between nestmate and non-nestmate eggs in *F. fusca* is the potential threat of intraspecific parasitism, which occurs when a founding queen takes over an established conspecific colony and hijacks its workforce. Low relatedness among *F. fusca* nestmate queens (Hannonen et al. 2004; Bargum et al. 2007) and the fact that even larvae seem to discriminate between nestmate and non-nestmate eggs (Pulliainen et al. 2019) support the idea that intraspecific parasitism shapes discrimination abilities in this species. Together, these results underline that phylogeny, ecology and within-colony social context are major factors mediating conspecific brood discrimination.

Interactions with heterospecifics

Ants are known to accept and rear heterospecific brood (Table 3). At the same time, the preference for familiar brood, especially when given a choice between con- and heterospecifics, is generally high, and pupa-carrying assays have been used as a taxonomic tool (Rosengren and Cherix 1981; Rosengren et al. 1994; Maeder et al. 2005). In addition, patterns of discrimination against heterospecific brood mirror phylogeny to a certain extent, so that more closely related species are more likely to rear each other's brood (Carlin 1988). Clearly, ant workers are capable of recognizing and discriminating against heterospecific brood. However, if they do so, depends on ecological context and the biology of the species.

The ability to discriminate against foreign brood is especially important in species that are targeted by heterospecific ant social parasites. These are numerous in ants and fall into three groups: permanentinquilines, slave-makers, and temporary social parasites (Hölldobler and Wilson 1990; Buschinger 2009). While permanentinquilines coexist with the host species, slave-making ants raid other colonies to capture and enslave their brood (Hölldobler and Wilson 1990; d'Ettorre and Heinze 2001). Queens of temporary social parasite species invade host colonies, kill the host queen(s), and take advantage of the brood care behavior of host workers to rear their eggs (Buschinger 2009). In all three cases, hosts may benefit from the ability to discriminate against parasite brood. However, this ability appears to vary among potential host species, and discriminatory behavior can be influenced by social context, e.g., the presence of conspecific brood. In addition, the identity of the intruder plays an important role in determining whether discrimination occurs. For instance, some hosts of slave-making species do not discriminate against brood of the slave-maker but do discriminate against other heterospecific brood (Alloy and Hare 1989; Zimmerli and Mori 1993; Mori et al. 1996). Failure to discriminate against parasite brood may be linked to chemical similarity between host and parasite brood (Lenoir et al. 2001b; Johnson et al. 2005). Such chemical deception is also employed by non-ant parasites such as *Maculinae* butterfly larvae, whose odors closely resemble those of the larvae of its ant host (Akino et al. 1999). However, not all parasite brood mimics host odors. For example, the pupal profiles of the slave-making ant *Protomognathus americanus* and its hosts (*Temnothorax longispinosus*, *T. curvispinosus*, *T. ambiguus*) are highly divergent (Achenbach et al. 2010), and hosts may use this information to discriminate against slave-maker brood (Achenbach and Foitzik 2009). Hosts and their parasites are typically locked in an evolutionary arms race, with hosts under selection to detect and remove parasites, and parasites under selection to avoid detection (Davies et al. 1989). The dynamics of such systems

may explain differences in brood discrimination behavior between species.

The complexity of host–parasite interactions and how they influence discrimination is perhaps best exemplified by studies of the ant *Formica fusca*. This species is a common host to temporary social parasites, whose queens found their colonies in the host nest (Punttila 1996). In populations with high parasite pressure, *F. fusca* exhibits excellent discrimination abilities, and both adult workers and larvae can discriminate against non-nestmate conspecific and heterospecific eggs (Helanterä and Sundström 2007; Helanterä et al. 2007, 2014; Helanterä and Ratnieks 2009a; Chernenko et al. 2011, 2013; Martin et al. 2011; Pulliainen et al. 2019), most likely with the help of colony-specific egg odors (Helanterä and d’Ettorre 2014). Whether discrimination actually occurs depends on factors such as queen presence and exposure of young workers to foreign odors (Helanterä and Sundström 2007; Helanterä et al. 2007; Helanterä and Ratnieks 2009a; Chernenko et al. 2013). In contrast, in populations without parasites, worker discrimination abilities as well as chemical diversity of egg surface cues are strongly reduced (Martin et al. 2011). Thus, in this species, discrimination against social parasites is mediated by the interaction of colony phenotype, worker ontogeny and species community ecology. Population-specific patterns of parasite brood discrimination have been demonstrated in other species (Achenbach et al. 2010; Solazzo et al. 2013), indicating that local adaptation plays an important role in shaping discrimination behavior.

Brood recognition: the importance of context

Recognition and discrimination in ants are highly context-dependent (Fig. 1). As it stands, it is sometimes difficult to disentangle whether the species-specific differences in brood discrimination reviewed here are phylogenetically determined or rather due to differences in ontogeny, ecology, or experimental design. For example, the references outlined in Tables 1, 2 and 3 illustrate that phylogeny is not a clear-cut determinant of brood recognition and discrimination abilities, as species belonging to the same genera (e.g., *Myrmica*, *Formica*) can differ immensely in their behavioral responses, even when they occupy similar ecological niches. In the final section of our review, we highlight ecological and experimental factors that have been shown to influence discrimination processes, and which may explain some of the contrasting patterns observed in previous studies.

Queen presence and number

The presence of the queen(s) has an important impact on key aspects of colony life such as worker reproduction and

female caste determination. Queen presence can also influence the brood recognition and discrimination behavior of workers (Brian 1973b, c; Vargo and Fletcher 1986; Edwards 1991; Passera et al. 1995; Klobuchar and Deslippe 2002; d’Ettorre et al. 2004; Helanterä and Sundström 2007; Vienne et al. 2010; Villalta et al. 2016). Compared to queen-right colonies, orphaned *Formica fusca* colonies for instance discriminate less against conspecific non-nestmate (Helanterä and Sundström 2007) and heterospecific eggs (Chernenko et al. 2013).

Monogynous (one reproductive queen) and monodomous (one nest) colonies may exhibit better nestmate discrimination abilities compared to polygynous and polydomous colonies (Sundström 1997; Martin et al. 2009). In the context of brood discrimination, experiments with the socially polymorphic ant *F. selysi* indicate that this is linked to differences in brood odor profiles from monogynous and polygynous nests, and not to differential discrimination abilities of monogyne and polygyne workers. In this species, workers from both monogyne and polygyne colonies were able to discriminate against foreign monogyne eggs, whereas neither was able to discriminate against foreign polygyne eggs (Meunier et al. 2010, 2011), suggesting that queen number influences signalers more than receivers. Concordantly, the hydrocarbon profiles of eggs are specific to social origin, so that polygyne eggs, more often than monogyne eggs, lack reliable colony-specific cues. Similarly, *Formica lugubris* workers from monogyne but not polygyne colonies show a slight preference for nestmate eggs (Maeder et al. 2005), but whether this is linked to egg surface chemistry is not known. Overall, cue scrambling in polygyne eggs may have evolved to prevent workers from discriminating between eggs from different matrilineal colonies in polygyne colonies (but see Helanterä and d’Ettorre 2014). This is in line with evolutionary predictions that kin-informative cues should be selected against to avoid colony-level costs associated with kin-preferential treatment (Ratnieks 1991; Keller 1997; Ratnieks et al. 2006).

Experimental constraints

There are several constraints that need to be considered when interpreting the results of discrimination studies. First, failure to detect discrimination does not necessarily translate into lack of recognition. Thus, even in studies that do not detect discrimination, workers may recognize brood of different origins but refrain from differential treatment (Pulliainen et al. 2018). Second, discrimination against brood is usually not an all-or-none process. Thus, the insight we gain from experiments testing only one type of brood (e.g., only heterospecific brood) are limited, since worker preferences may change when they are given a choice, for instance between con- and heterospecific brood. For example, *Leptothorax nylanderii* and *Tapinoma erraticum* workers fail to discriminate against

heterospecific brood when no other brood is present but show a clear preference for conspecific brood when con- and heterospecific brood are presented simultaneously (Plateaux 1960a; Meudec 1978). Furthermore, even though alien brood may at first be accepted, discrimination can still occur, for instance in the form of later neglect or consumption (Jaisson 1975; Jaisson and Fresneau 1978; Le Moli and Passetti 1978; Johnson et al. 2005; Chernenko et al. 2011, 2013). The conditions under which brood are obtained for experiments may also affect experimental outcomes: in *Neoponera inversa*, eggs from lab and field colonies differ in their cuticular profiles. When worker-laid eggs sampled from lab colonies were treated with a synthetic queen-derived compound, they elicited aggressive treatment by workers. In contrast, worker-laid eggs from field colonies treated with the same compound did not elicit worker aggression (van Zweden et al. 2009b).

Third, discrimination tests in the past have often used frozen rather than fresh brood. This can have a strong effect on the way workers treat brood. *Atta cephalotes* workers for instance retrieve living larvae significantly more often than dead larvae but do not seem to distinguish between dead and living pupae (Robinson and Cherrett 1974). Using dead brood may affect worker behavior if discrimination is based on acoustic signals (as appears to be the case in *Myrmica scabrinodis*, Casacci et al. 2013), or if workers use behavioral cues to recognize brood. This may be especially relevant in the case of discrimination of larvae, since this is the only mobile developmental stage. Indeed, even though *A. cephalotes* workers differentiate between dead and live larvae, they do not react to odor extracts from live larvae (Robinson and Cherrett 1974), suggesting that larval behavior, not odor, is crucial for recognition in this species.

Finally, special care must be taken to avoid confusing brood retrieval behavior with other behaviors, in particular food foraging behavior. This may be especially relevant in cases, where colonies have been starved prior to experiments, since brood represents an excellent food source. Furthermore, ant foragers can use chemical cues to identify suitable food items, and these cues may overlap with brood chemical cues (Viana et al. 2001). Specificity of brood cues has been a much-discussed challenge in the field (Walsh and Tschinkel 1974; Morel and Vander Meer 1988; Vander Meer and Morel 1988), and we refer the interested reader to Tschinkel (2006), who thoroughly reviewed the data on brood recognition cues in fire ants, the best studied ant species in this (and many other) respects.

Conclusion

Our review of the literature has shown that, while brood discrimination is generally less stringent than discrimination against adults, it can be important in a number of

fitness-related contexts. Carlin (1988, page 283) summarized four features of brood recognition in ants: “(1) potent generalized brood stimuli, (2) sufficient similarity in brood stimuli to facilitate acceptance across kin, colony and species categories, (3) sufficient variation in brood stimuli to enable non-exclusive discrimination of kin, nestmates and species and (4) learned recognition of colony- and species-specific variants of the stimuli.” To these, we can now add (5) sufficient variation in brood stimuli to enable discrimination according to viability, developmental stage, sex, and caste, (6) strong context dependency and influence of individual phenotype and social environment, and (7) wide diversity in brood stimuli, including brood surface chemistry, secretions, morphology, and behavior, that can act alone or together. In spite of these advances, many open questions remain about brood-directed behavior, and more generally, about social interactions involving brood in ants. As the role of development in driving evolutionary processes receives more attention, studies focusing on brood–adult interactions are beginning to provide insight into the physiological and genetic mechanisms underlying these complex interaction networks (Chandra et al. 2018; Walsh et al. 2018b; Warner et al. 2019) and their evolutionary basis (Walsh et al. 2018a). Hopefully, this review will help inspire future research on the fascinating life of ant brood.

Acknowledgments Open Access funding provided by Projekt DEAL. This work was supported by the Bayrisches Staatsministerium für Bildung und Kultus, Wissenschaft und Kunst (E.S.) and the LUOVA Doctoral Programme (U.P.). The authors thank Jan Oettler, Jürgen Heinze, Miriam Richards and two anonymous reviewers for comments on previous versions of the manuscript.

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