Laura Aquiloni · Elena Tricarico *Editors*

Social Recognition in Invertebrates

The Knowns and the Unknowns

Springer

Social Recognition in Invertebrates

Laura Aquiloni · Elena Tricarico
Editors

Social Recognition in Invertebrates

The Knowns and the Unknowns

Springer

Editors
Laura Aquiloni
Department of Biology
University of Florence
Florence
Italy

Elena Tricarico
Department of Biology
University of Florence
Florence
Italy

ISBN 978-3-319-17598-0 ISBN 978-3-319-17599-7 (eBook)
DOI 10.1007/978-3-319-17599-7

Library of Congress Control Number: 2015936295

Springer Cham Heidelberg New York Dordrecht London

Printed on acid-free paper

Springer International Publishing AG Switzerland is part of Springer Science+Business Media
(www.springer.com)

To Francesca Gherardi
who liked taking up challenges
and breaking new grounds

Foreword

Presentation of "Social Recognition in Invertebrates"

Social recognition, awareness and personality are all concepts that derive from human sciences and therefore are not universally accepted when applied to animals. Nevertheless, from the beginning of the study of animal psychology and behaviour, ethologists have used these concepts, after having re-defined them to avoid any anthropomorphism (Köhler 1925; Bierens De Haan 1929, 1951; Lorenz 1932, 1988). The fear for anthropomorphism dates back to the scientific revolution, since the Cartesian mechanism separated humans and animals, being the latter explicable only in terms of machines (Scapini 2010). Evolutionary biology has reintroduced gradualism in the stream of life, stressing on the continuity of all the organisms, and particularly animals and humans through apes. In the light of Darwinism, the studies on animal behaviour do not have a-priori barriers for the use of the above cited concepts, and this has favoured enormous progress in primatology and the study of social vertebrates. The question of animal awareness was posed in the context of evolutionary continuity and a parsimonious explanation of behaviour (Griffin 1976). However, invertebrates are apparently still representing "another word", where mechanical concepts are preferentially applied, following the Cartesian heritage, such as the theory of taxes in animal orientation (e.g., Fraenkel and Gunn 1961). The question is still open whether the lack of evidence of higher capacities in invertebrates derives from the animal apparently simple organisation or from a non-adequate experimentation. The late Francesca Gherardi, an outstanding experimental ethologist, asked questions to the animals selves, by ideating experiments without theoretical prejudice. So she succeeded in showing unexpected "cognitive" capacities in hermit crabs and crayfish, including individual behavioural syndromes, defined as "personality", and individual recognition that implies self-awareness (citations in Hazlett, this volume).

The contributions of the present book are focussed on the behaviour of major invertebrate groups, namely insects (termites, coleopterans, hymenopterans) and crustaceans (stomatopods, amphipods, decapods), which is a challenge in the context of cognitive capacities. They provide theoretical and experimental bases for a new insight in this debated context. The theoretical bases have as start points both the phylogenesis and ecology of the analysed animal taxa, which represents the necessary background for further research. This is integrated by the description of the state of art of experimental evidence in social recognition in each taxon. For the nature of experimental research, the latter part is extremely variable among chapters, opening more questions than solving ones, which is perfectly scientific. A good scientist always doubts on solved questions; science is always approximation, tending to enhance insight. Driven by the revisitation of social recognition by Gherardi et al. (2012) the authors of the book chapters made a common effort to identify the questions to which the experiments could respond.

What appears striking in the evidence provided by this book, is the fact that the highest cognitive capacities in social recognition were not found in insects with established societies, but more in solitary insects and crustaceans that strive to chase conspecifics from resources. The importance of behavioural flexibility in individual interactions is evident here: in an established society individuals have their roles, behaving exactly as they should, while in an hostile surrounding, both physically and biologically harsh, the individual animals have to continuously adapt to novel situations, therefore the recognition of a potential enemy or mate is adaptive. The capacity of learning about a new context is of extreme importance in any animals that live in changeable environments and behavioural plasticity is here a pre-requisite. Behavioural plasticity has been recognised as a key concept in several contexts at all levels of organisation (e.g., Menzel and Giurfa 2001; Briffa et al. 2008; Scapini 2014).

The communication channel/s used in social recognition tasks is a frequently debated question: whether the best adaptation requires one dedicated channel (chemical, visual, or mechanical…) or multiple channels are used in social recognition. The advantage of using visual instead of chemical clues is clear, but may derive from human prejudice (humans use preferentially visual clues for social recognition), but more experimental research in different animal groups is needed to clarify this point. The multiple channel strategy is apparently safer and may be advantageous both in interspecific and intraspecific aggressive interactions. Also for this question, a sound knowledge of the species ecology is necessary.

On the whole this book is very useful to encourage experiments testing new questions on the various sociality levels of different animal groups. The outcome is extremely interesting for the broad range of examples and contexts presented in the various book chapters, as well as for the scientific rigour together with the absence of any prejudice, both very important for progress in science.

Felicita Scapini

References

Bierens De Haan JA (1929) Animal Psychology for Biologists. University of London Press, London

Bierens De Haan JA (1951) Psicologia degli animali, Arnoldo Mondadori Editore, Verona (Italian translation of Animal Psychology), pp 161

Briffa M, Rundle SD, Fryer A (2008) Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus.* Proc R Soc B 275(1640):1305–1311

Gherardi F, Aquiloni L, Tricarico E (2012) Revisiting social recognition systems in invertebrates. Anim Cogn 15:745–762

Griffin DR (1976) The question of animal awareness, evolutionary continuity of mental experience. The Rockfeller University Press, New York, pp 135

Fraenkel GS, Gunn DL (1961) The orientation of animals—kineses, taxes and compass reactions. Dover Publications, New York, pp 376

Köhler W (1925) The mentality of Apes. Harcourt, New York

Lorenz K (1932) Betrachtungen über das Erkennen des arteigenen Triebhandunglen der Vögel. J Ornithol 80 (1):50–98

Lorenz K (1988) Hier bin ich – wo bist du ?, R. Piper GMbH & Co. KG, München (Italian translation Io sono qui – tu dove sei?, Arnoldo Mondadori Editore, Frigliano, CN, 1990, pp 259)

Menzel R, Giurfa M (2001) Cognitive architecture in a mini-brain: the honeybee. Trends Cogn Sci 5:62–71

Scapini F, Hoppe B (2010) Zoology, Brill's encyclopedia of the ancient word New Pauli—classical tradition. Brill, Leyden, pp 1138–1183

Scapini F (2014) Behaviour of mobile macrofauna is a key factor in beach ecology as response to rapid environmental changes. Estuarine, Coast Shelf Sci 150:36–44

Preface

Social Recognition in Invertebrates: An Introduction for the Readers

Social recognition is regarded as a key element in life of many organisms, where it can play an essential role in the structure and stability of a number of behavioural networks, such as dominance hierarchies, territorial defence, competitive aggression, pair bonds, mate selection, and kin favouritism. The skill for sophisticated and flexible recognition—as for cognitive abilities—has been known for a very long time in vertebrates, particularly in mammals, who are the most closely related to humans and from which there is an expectation to provide some insights for human evolution, being their behaviour easily recognized. However, as evidenced by the growing number of studies and reports, there is an increasing scientific interest in the occurrence and properties of this ability in invertebrates where, however, it may not be so easily and clearly identified. The possible presence of individual recognition as well as the communication media and cues involved in social recognition is the prevalent topic of recent studies, indicating that invertebrates can possess refined recognition systems and that, regardless of their taxonomic status, many animals show sophisticated recognition abilities. The present book offers a compendium of the most recent advances of social recognition in invertebrates, dealing with several behaviours involved in this recognition as cooperative behaviour, parental care, mating and aggressive relationships.

Among invertebrates, eusocial insects (ants, wasps, termites and bees) represent the most fascinating examples of cooperative group living and surely the most studied since 1950s for the evolution of cooperative behaviour and recognition systems. The incredible organization of a social insect colony is based on the ability to recognize and assign individual membership to a particular and relevant class, such as caste, dominance status and gender, and on the discrimination between nestmates from non-nestmates (reviewed in this volume by Bagnères and Hanus; Breed et al.; Cervo et al.). The ontogeny of this nestmate recognition is a still open and fascinating field: according to Signorotti et al. (this volume), wasps and bees seem to learn the recognition cues required for template formation from their nest/comb odour, while ants learn principally from their nestmates. To avoid errors, the chemical referent template is updated during life, indicating a learning and plastic process, particularly useful for social parasites (Signorotti et al., this volume). Also burying beetles, due to their key features—the extended biparental care and the reproduction on dead vertebrates- evolved sophisticated recognition mechanisms, as recognition of a conspecific sex, the previous mating partner, the breeding partner, including its reproductive state, and the offspring (Steiger, this volume). In insects, social recognition is generally considered to be mediated by chemicals (Breed et al.; Signorotti et al.; Steiger, this volume), and numerous progresses have been achieved in understanding the identity, origin and production of these recognition cues in social hymenoptera. Nevertheless, recent discoveries indicated that visual signals can be relevant in some species of social wasps for several social behaviours (Cervo et al., this volume), and, even in termites, vibration-based signals complement the chemical cues (Bagnères and Hanus, this volume).

Besides, chemical cues are important in social communication of crustaceans, the other most studied taxon among invertebrates for social recognition. Historically, hermit crabs (Hazlett, this volume) and stomatopds (Vetter and Caldwell, this volume) awakened the interest of individual recognition in invertebrates, showing the first evidences of this ability in this group, considered for long time not suitable for this complex phenomenon. In hermit crabs, researchers found a reliable behavioural essay (the explorative behaviour of a test shell in the presence of different odours) that allowed the investigation of this aspect, particularly in dominance interactions (Hazlett, this volume). In stomatopods, the presence of individual recognition was clearly demonstrated both in territorial defence and in reproductive contexts, being mantis shrimps able to recognize also current mates and young, and to avoid previous mates (Vetter and Caldwell, this volume). Individual recognition has been proved in lobsters, but only suggested in crayfish, widely studied for their dominance relationships and mate recognition (Patullo and McMillan, this volume). All forms of social recognition and interspecific communication have been documented in shrimps, including recognition by mate, size, rank, kin and individual (Solomon et al., this volume). On the contrary, in amphipods, despite the great opportunities they have for their social life-style (dense aggregations, cohabitation with mating partners for long time periods, or in family groups), data on their social recognition are still scanty and up-to now limited to mate and female-offspring recognition (Berman et al., this volume). The matter of the multimodal communication in social recognition of crustaceans is emerging as an intriguing research topic: stomatopods have the most advanced vision in Crustacea and can use visual cues and auditory ones ("the click") in aggressive interactions (Vetter and Caldwell, this volume). Crayfish can couple chemical and visual (and sometimes tactile) cues for the establishment of the hierarchies and the mate selection. However, the message conveyed by the single medium as well as the nature of chemical cues should be still clarified and identified (Patullo and McMillan, this volume).

New invertebrates are eliciting the scientific attention for social recognition, as the annelids, which behavioural interactions are mostly unexplored (Lorenzi et al., this volume). Many annelids use chemical and visual cues to locate partners and classify them according to mating status, body size, oocyte ripeness or belonging to same or a different population, but only few pheromones for mate recognition and gamete release have been identified.

Surprisingly, little experimental data exist on social (and individual) recognition among octopuses (not present in this volume), despite their unusual cognitive abilities due to the refined neuronal organization and vertebrate-like behavioural machinery they have. Based on the available knowledge, Boal (2006) concludes that there is no robust experimental evidence for assuming the capability of recognition of species, offspring or kin in cephalopods. However, some examples may provide insights for future studies. Among octopuses, individuals of *Octopus bimaculoides* are reported to be able to distinguish same- from opposite-sex on the odour as suggested by measures of changes in ventilation rate (Boal 2006). On the other hand, males of *Hapalochlaena lunulata* approach and attempt to mate either female or male conspecifics (Cheng and Caldwell 2000). Several species are known to use body patterning as defence systems (e.g. camouflage) but also as an intra-specific means of communication, mostly in the contexts of fight and mating (reviewed in Tricarico et al. 2014). Recently, Tricarico et al. (2011) showed that *Octopus vulgaris* can recognize conspecifics and can discriminate (and remember) familiar from unfamiliar individuals. This means that this species is able of, at least, class-level or binary individual recognition (Tibbetts and Dale 2007), an ability never found in other cephalopod species. The ability to recognize and remember ‘opponents’ and conspecifics may have an adaptive value for *O. vulgaris*, being the likely proximate mechanism regulating the “dear enemy phenomenon” and possibly explaining the scarcity of interactions between octopuses, as observed in the field. Despite the needs of more in depth studies needed to clarify whether *O. vulgaris* is able of true individual recognition, the study by Tricarico et al. (2011) is to the best of our knowledge the sole reporting conspecific social recognition in cephalopods (see Boal 2006 for a review). Finally, it is noteworthy to report that Anderson et al. (2010) noted that octopuses are also capable to recognize the caretakers in the laboratory. Recognition of humans among animals is a peculiar capability reported in a few species that, if confirmed in octopus, may further provide evidence of the peculiarity of these animals among other invertebrates. Concerning other molluscs, we have scanty information: the presence of species recognition was found in the slug *Limax grossui* (an individual follows the mucus trails of conspecifis: Cook 1977), while in *Aplysia fasciata* the ink seems to be used as a social cue during intraspecific interactions (Fiorito and Gherardi 1990).

The Way Ahead

This volume shows that several studies have now been conducted on a wide range of invertebrates to investigate the different behaviours and aspects of their social recognition, leading to new discoveries and advances. Insects and crustaceans as crayfish, hermit crabs, shrimps and stomatopods have proven themselves to be excellent model studies for this topic. Anellids and amphipods are emerging as promising taxa for future studies, while molluscs, particularly cephalopods, could reveal great surprises when coming out from the "grey area". However, the number of considered invertebrates is still low, despite this group comprises the majority of animal species on the earth. The adopted experimental procedures appear to be sometimes limited for several reasons (no reliable behavioural essay or lack of certainty on observed behaviours and/or used communication media and signals), and should be thus improved. Today, individual recognition, ontogeny of nestmate recognition and social multimodal communication are the great expectations of social recognition in invertebrates. As stated by Gherardi and colleagues in 2012 "The way ahead may be long, but the promises of disclosing unexpected cognitive abilities in this extremely vast and diversified assemblage of animals make it worth being followed."

Laura Aquiloni
Elena Tricarico

References

Anderson RC, Mather JA, Monette MQ, Zimsen SRM (2010) Octopuses (*Enteroctopus dofleini*) recognize individual humans. J Appl Anim Welfare Sci 13:261–272

Boal JG (2006) Social recognition: a top down view of Cephalopod behaviour. Vie et Milieu 56:69–79

Cheng MW, Caldwell RL (2000) Sex identification and mating in the blue-ringed octopus, *Hapalochlaena lunulata.* Anim Behav 60(1):27–33

Cook A (1977) Mucus trail following by the slug *Limax grossui* Lupu. Anim Behav 25:744–781

Fiorito G, Gherardi F (1990) Behavioural changes induced by ink in *Aplysia fasciata* (Mollusca: Gastropoda): evidence for a social signal role of inking. Mar Behav Physiol 17:129–135

Gherardi F, Aquiloni L, Tricarico E (2012) Revisiting social recognition systems in invertebrates. Anim Cogn 15:745–762

Tibbetts E, Dale J (2007) Individual recognition: it is good to be different. Trends Ecol Evol 22:529–537

Tricarico E, Borrelli L, Gherardi F, Fiorito G (2011) I know my neighbour: individual recognition in *Octopus vulgaris*. PlosOne 6(4):e18710

Tricarico E, Amodio P, Ponte G, Fiorito G (2014) Cognition and recognition in the cephalopod mollusc *Octopus vulgaris*: coordinating interaction with environment and conspecifics. In: Witzany G (ed) Biocommunication of animals. Springer, Berlin, pp 337–349

Contents

Chapter 1
Social Recognition in Annelids and the Evolution of Social Recognition and Cognitive Abilities by Sexual Selection

Maria Cristina Lorenzi, Stefania Meconcelli and Gabriella Sella

Abstract Social recognition has rarely received attention in the studies on annelids. This is not surprising since the biology of behavioral interactions in annelids is mostly unexplored. Only few pheromones have been identified, which function as cues in mate recognition and gamete release. Many annelids use chemical and visual cues to locate partners and classify them according to mating status, body size, or oocyte ripeness. In some hermaphroditic polychaete worms and leeches the ability to recognize the quality of potential partners seem to be very refined, especially in relation to the ability to assess the number of competitors over mating. These examples suggest that sexual selection might have favored individual ability to assess conspecific numerosity accurately and vary their male and female resource allocation (sex allocation) accordingly. Finally, annelids can estimate whether they are related to their potential partners and whether they belong to the same or a different population, which again result in adjustments of their reproductive allocation. We suggest that sexual selection is likely to be responsible for the evolution of the ability to assess mate quality and social group size because sex allocation adjustments are favored by sexual selection.

M.C. Lorenzi (✉) · S. Meconcelli · G. Sella
Department of Life Science and System Biology, University of Turin, via Accademia Albertina 13, Turin, Italy
e-mail: cristina.lorenzi@leec.univ-paris13.fr

S. Meconcelli
e-mail: stefania.meconcelli@unito.it

G. Sella
e-mail: gabriella.sella@unito.it

M.C. Lorenzi
LEEC-Laboratoire d’Ethologie Expérimentale et Comparée,
Université Paris 13, Sorbonne Paris Cité, 99 avenue J.-B. Clément, Villetaneuse, France

L. Aquiloni and E. Tricarico (eds.), *Social Recognition in Invertebrates*,
DOI 10.1007/978-3-319-17599-7_1

Keywords Earthworms · Leeches · Polychaete worms · Mate choice · Mating group-size · Mate relatedness · Kin recognition · Sexual selection · Sperm competition · Numerosity

Introduction

Social recognition has rarely received attention in the studies on annelids. This is not surprising since the biology of behavioral interactions in annelids is mostly unexplored. Additionally, there may be a cultural prejudice going back to Darwin that annelids have limited cognitive abilities. Indeed, as Velando et al. (2008) pointed out, Darwin (1871) evaluated the potential for sexual selection to occur in this way: “All these worm-like animals apparently stand too low in the scale for the individuals of either sex to exert any choice in selecting a partner, or for the individuals of the same sex to struggle together in rivalry” (Darwin 1871).

Darwin was convinced of the limited cognitive power of the “the lower classes” of animals, which had “too imperfect senses and much too low mental powers to appreciate each other’s beauty or other attractions, or to feel rivalry.” To Darwin, sexual selection could not work in worm-like organisms, including annelids. In the following pages we advance the opposite hypothesis: since there is evidence that sexual selection is at work in annelids (e.g., Sella 2006; Lorenzi and Sella 2008; Velando et al. 2008), here we suggest that sexual selection may have been a main selective force favoring the evolution of cognitive abilities including social recognition.

The Mechanisms Underlying Social Recognition in Annelids

The physiology underlying social recognition has been under scrutiny in vertebrates in the last decades (e.g., Salva et al. 2012), but is more rarely studied in invertebrates (but see, for example, Tibbetts and Dale 2007). Especially in annelids, our knowledge of the mechanisms at the basis of recognition is very poor. However, many annelids are equipped with an impressive array of sensory structures with which they gain information about their environment. Because the analysis of these structures would go beyond the scope of this book, we refer to the specialized literature for focused overviews (e.g., Purschke 2005). In general, for many marine organisms including annelids, chemical cues and chemoreception mediate many crucial behaviors including defense, reproduction, recruitment and feeding (reviewed by Zimmer and Butman 2000).

In polychaetes nuchal organs are primary chemoreceptive organs, but other complex chemosensory structures have also been described, such as dorsal and metameric ciliated organs and parapodial sensory structures (Lindsay 2009). There is also evidence of specialized visual sensory receptors. Species of the genera

Alciopa, *Torrea* and *Vanadis* possess image-resolving eyes (Wald and Rayport 1977). *Odontosyllis* worms have four eyes, which are located two per part on the two sides of the head. The eyes are on lobes that have some degree of movement, they reside in a cavity and have a lens, photoreceptor cells and pigment granules (Wolken and Florida 1984).

Little is known on the proximate mechanisms involved in social recognition in annelids. Linsday (2009) reviewed the main aspects of chemoreception in polychaetes. According to this author, only few pheromones have been identified, which are responsible for mate-recognition and gamete release. In the semelparous species *Nereis succinea* and *Platynereis dumerilii*, 5-methyl-3-heptanone induces the nuptial dance. The pheromone triggers its biological effect at different concentrations in the two species, thus ensuring reproductive isolation based on response threshold levels. Different threshold concentrations of the same compound convey different signals in *N. succinea* as well. Females release cysteine-glutathione-disulfide as a mate-recognition signal which attract males from long distances. A higher concentration of the same compound induces males to release sperm. Other identified pheromones are the egg-release pheromone inosine in *N. succinea* and the sperm-release pheromone uric acid in *P. dumerilii*.

Most of these substances are found in many marine invertebrates and their specific biological activity is mediated by concentrations. In this regard an interesting aspect of the sexual pheromones in nereid polychaetes is their activity across species (Hardege 1999; Watson et al. 2003). According to these Authors, extracts from the body fluids of some nereid species (as well as those from other marine invertebrates) induce spawning in other nereid species. Spawning by one species can activate mass spawning events involving multiple species, similar to those observed in the Great Barrier Reef, while coordination of spawning between conspecific partners is controlled by species-specific concentrations of the same compounds (Hardege 1999).

To Which Extent Are These Sensory Mechanisms Involved in Social Recognition?

To our knowledge, most social interactions in annelids occur during mating and reproductive interactions. Worms are able to locate potential partners and recognize each other from worms of other species, because strong prezygotic reproductive barriers impede interspecific mating in annelids. In some species, individuals are not only attracted to their partners, but they also discriminate between mature and non-mature partners or evaluate other, even more subtle, qualities of their partners. Annelids are present in a great variety of ecosystems: there are earthworms, sea worms, abyss worms and fresh water worms. This makes it possible the diversification of the sensory structures according to the environment and the life style of the animals.

Mate Choice Is a Component of Social Recognition

Social recognition is a sophisticated cognitive ability, which is advantageous in many social interactions, from encounters between partners during mating to complex social behaviors (Tibbetts and Dale 2007). Mate choice is a component of social recognition: it involves discriminating between classes of organisms (like conspecifics and non-conspecifics), between sexes (in separate sex species), and between potential partners according to their attractiveness, quality and/or relatedness (Sherman et al. 1997). In this respect mate recognition involves different kinds of class-level social recognition, i.e., recognition of classes of individuals (Gherardi et al. 2012).

Many annelids use chemical and visual cues to locate partners. For example, ripe females of the *Odontosyllis* species emit light flashes. Flashes might have multiple functions, but some observations suggest that females of the Bermudian fireworms *O. enopla* attract males by releasing luminescent secretions (Fischer and Fischer 1996).

Males of the marine polychaete worms *Ophryotrocha labronica* and *O. puerilis* (the latter is a sequential hermaphrodite) are attracted by water where females have spent some time, suggesting that females might release attractive substances in the water (Berglund 1990, 1991). Some annelids use cues to classify their partners according to mating status, body size, or oocyte ripeness. In dense populations of the hermaphroditic *Eisenia andrei* redworms multiple mating is common (Monroy et al. 2003). When redworms copulate with mated partners, their sperm compete with those of the previous partner(s) in egg fertilization. During courtship, redworms recognize their partner's mating status (i.e., whether they have already mated or not and whether they have/have not already received sperm from other partners). Indeed, redworms adjust the amount of sperm they donate to their partner according to the mating status of their partner (Velando et al. 2008). If partners have already mated and have sperm in their spermatheca, redworms transfer three times more ejaculate to their partners than that they do to non-mated partners, thus increasing the chances to fertilize eggs (Velando et al. 2008). This is not the only measure they take to estimate the quality of their partners. They also adjust the amount of donated sperm to the body size of their partner (prudent mating effort, Wedell et al. 2002; Anthes 2010). Large redworms usually have higher fecundity and receive twice the amount of ejaculate than small redworms (Velando et al. 2008).

Eisenia fetida and *Lumbricus terrestris* earthworms seem to be able to classify partners by body size as they mate preferentially with matching partners (size-assortative mating): variance in body weight and size within a pair is smaller than that between pairs (Michiels et al. 2001; Monroy et al. 2005). For example, *L. terrestris* use tactile cues during the pre-copulation phase to choose sexual partners. The courtship behavior consists of repeated mutual burrow visits between neighbors and during these visits partners maintain close contact while moving back and forth between their burrow openings. Michiels et al. (2001) advanced the hypothesis that body size is one of the qualities that earthworms assess during these visits to potential partners. Size is used in mate choice and influences the outcome of mating. Earthworms mate sooner with same-sized neighbors than with differently sized ones, and small earthworms visit large neighbors more often than small ones. When mates separate, one of them can be pulled out of its burrow and this mating outcome is more likely to occur to small individuals. Therefore, in *L. terrestris*, mate assessment is reached by assessment of body size by contact.

Overall, these findings suggest that in earthworms mating is not random and mate choice or ejaculate size are adjusted to partner characteristics or quality. Although the cues that earthworms use to assess their partner conditions (body size or mating status) are largely unknown, these data document that earthworms have an efficient recognition system that can be used for mate evaluation (Domínguez and Velando 2013). Additionally, because there are no processes other than mating which involve interactions between individuals in redworms, these data suggest that sperm competition (a post-copulatory component of sexual selection) might have favored earthworms that have the ability to recognize their partner's quality, to process and to use this information appropriately. Thus, sperm competition favors earthworms that have some cognitive abilities.

The gonochoric nereidid polychaete *Neanthes acuminata* provides evidence for sophisticated mate choice. *N. acuminata* females mate only once, are semelparous and die soon after laying eggs, whereas males care for the developing eggs. As expected in semelparous organisms, females assess male quality very accurately. In particular, since egg survival largely depends on the male ability to care for eggs, paternal egg-caring is a crucial male trait. Fletcher et al. (2009) showed that females classify males based on their experience in egg-caring, and prefer to mate with experienced rather than naive males, even when naive males had low success in male-male fights that often occur in these populations. This suggests that females exhibit mate choice on the basis of the good-parent model of sexual selection (Storey et al. 2013). The choice of the partner is based on transient chemical signals that females recognize as a 'scent of experience' (Storey et al. 2013).

In the polychaete worms of the genus *Ophryotrocha* assessment of mate qualities occurs by means of tactile and/or chemical cues. The sequential hermaphroditic worms *O. puerilis* are sex-changers: they start their sexual life as males and turn into females when they reach a certain body length (Berglund 1986). Laboratory experiments have shown that females prefer small males as mates and reject large males, possibly to avoid prospective sexual conflicts (Berglund 1990). Large males may be more likely to switch to the female sex and if that happens, the pair will be composed of two females. According to Berglund (1990), size is the crucial cue behind female choice; larger individuals could be recognized as females and smaller ones as males. We do not know how these worms assess their partner body size (e.g., through tactile and/or chemical cues). However, partners may control (or manipulate) reciprocal sex changes (Grothe and Pfannenstiel 1986). When the male partner turns to the female sex, one of the two females now forming the pair will switch back to the male sex. This form of alternating sex change requiring continuous recognition of the current sexual phenotype of the partner is present in other hermaphroditic annelids (*Helobdella* and *Syllis*).

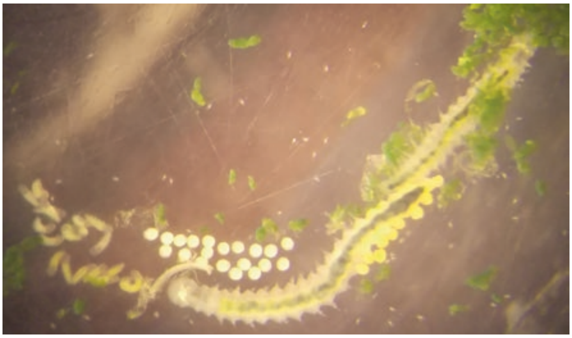


Fig. 1.1 A pair of *Ophryotrocha* worms with cocoons containing eggs or larvae

The ability to discriminate between the sexual phenotypes of the potential partners (i.e., to perform not an individual- but a class-level social recognition) is present also in the non-selfing, iteroparous, simultaneously hermaphroditic species *O. diadema* and *O. gracilis* (Fig. 1.1). In these species, the hermaphroditic phase is preceded by an adolescent male phase. Mature hermaphrodites identify the physiological status of potential partners, and generally form pairs with simultaneous hermaphrodites after a time-consuming courtship, whilst adolescent males are discarded as partners (Sella 1990). In isolated pairs, hermaphrodites regularly take turns in playing either the male or the female role during successive mating events, so that they trade eggs for sperm, and individuals retaliate when partners do not lay eggs in their turn, by stopping egg laying (Sella 1985). Reciprocal egg-exchanges occur only if the same two individuals interact repeatedly and, in theory, such conditional reciprocity requires that partners recognize each other either individually or as familiar partners (Axelrod and Hamilton 1981). Indeed, conditional reciprocity is an evolutionary solution to conflicts over sexual roles in simultaneous hermaphrodites (Leonard 2005), but cheaters exist that repeatedly mate in the male role (Di Bona et al. 2010). In these conditions, selection should have favored reciprocating individuals that identify cheaters and retaliate against them, as was shown by Sella (1988). Reciprocating pairs usually spend most of their time in caring for their egg cocoons, which they often lay in a sort of nest site, where mucous trails are dense. However, occasionally one or both worms leave their nesting site, e.g., for foraging. When nesting sites are unattended, or when only one worm is there, cheaters could enter the nesting sites, pretend to mate in the male role and leave. Cheater success would be limited, and cheater strategy would not spread in evolutionary times, only if partners recognize each other through individual or familiar recognition. In stable pairs, familiarized partners have shorter inter-spawning time intervals than unfamiliar worms have, which suggest some form of partner recognition. Each worm could either recognize its partner through individual characteristics or, more likely, could learn some individual trait of familiarized partners (e.g., odor). There has been only one experimental test for such ability, but the experiment failed to prove that *O. diadema* worms recognize the individual with which they have previously traded eggs (Lorenzi and Sella 2000). After a period of familiarization between paired partners, partners were separated for a short period, and then pairs were formed again between either familiar or unfamiliar partners.

Both kinds of pairs had similar inter-spawning intervals, suggesting that there was no recognition of familiar partners (Lorenzi and Sella 2000). Of course, it is possible that the experimental manipulation was stressful in itself, and worms had to recover from the experimental manipulation before being able to spawn again, irrespective of any partner recognition ability.

Recognition of Social Group Size

Current evolutionary theory makes specific predictions about the abilities of organisms to measure the presence and number of potential competitors over mating. For example, variations in the level of competition for egg fertilization (i.e., sperm competition) should affect the quality and/or amount of resources that males devote to sperm or other male traits (Parker 1998), but this requires that males be able to assess the number of competitors over the male role, i.e., that they recognize their potential rivals, such as mature males, among their conspecifics. Sex allocation theory makes similar predictions: hermaphrodites are expected to adjust their sex allocation to mating group size, i.e., to the number of potential mates (Charnov 1982). According to theory, when the number of mates is small, hermaphrodites allocate few resources to sperm production and devote their remaining resources to egg production. As the number of mates increases, hermaphrodites increase the amount of resources devoted to the male function at the expenses of those available to the female function (Charnov 1982; Schärer 2009 for an updated review). In other words, they adjust their male function to current level of mate competition, trading off resources between the two sexual functions. In experimental practice, mating group size is technically difficult to measure, and therefore social group size is often used as a proxy, under the hypothesis that the larger the social group, the stronger the competition for mating. We are not interested in sex allocation theory here, but in the ability of hermaphrodites to measure the size of their group in order to adjust their sex allocation to social group size.

To adjust sex allocation to current social conditions, hermaphrodites have to perceive the intensity of mate competition they are likely to encounter, i.e., they have to estimate their mating opportunities and change the amount of resources allocated to their sexual functions appropriately. Mating opportunities are likely to increase with increasing group size. Therefore, hermaphrodites might have been selected to be able to measure their group size, i.e., the numerosity of the conspecifics in a population or neighborhood. We recall that in simultaneous hermaphrodites each individual is both a potential mate and a potential rival. Although the ability to assess group size may be common to hermaphrodites in other taxa, in annelids there are a few interesting examples. In the leech *Helobdella papillornata,* juveniles adjust the volume of their testisac (a sac around the testis) to the social group size they experience during development; the testisac is larger when group size is larger. Here, juveniles use the size of the social group as a proxy for the intensity of sperm competition they will encounter in their adult life (Tan et al. 2004). Hermaphroditic polychaetes of the genus *Ophryotrocha* can make even more precise estimates of their social group size. Most of these worms live at low densities, but populations vary in size (Simonini et al. 2009). In larger or denser groups, multiple paternity of single egg-clutches is common, as a consequence of multiple matings and competition among sperm of different males (Lorenzi et al. 2014). As adults, these worms adjust their female allocation to social group size (which, again, is likely to be a proxy for mating opportunities). These hermaphrodites estimate how many of them there are, and make this measurement irrespectively of the density of worms (i.e., irrespectively of the number of worms per units of water volume) or of metabolite accumulation (Lorenzi et al. 2005). Experimental evidence suggests that in a few days they can both make these measurements and adjust their female allocation appropriately, but they are also ready to re-adjust it quickly, should group size change again (Lorenzi et al. 2008, Lorenzi pers. obs.). Using female-allocation adjustment as a proxy for the ability of these worms to assess group size, we found evidence that these worms make a more precise estimation of group size for small than for large sizes, but precision is also likely to depend on species-specific conditions under which the different species have evolved. For example, both *O. adherens* and *O. diadema* worms allocate their resources to the female function depending on whether they are in groups of 2, 4, or 12 hermaphrodites (Fig. 1.2a). However, the sizes of their adjustments are different. *O. diadema* hermaphrodites respond more to changes in social group size from 2 to 4 than to changes from 4 to 12 hermaphrodites. In contrast, *O. adherens* hermaphrodites respond more to group-size changes from 4 to 12 than to changes from 2 to 4 hermaphrodites (Fig. 1.2b). This suggests that worms make more precise assessments of group size within certain ranges of variation than others, either because they are more precise in their estimates of group size or because they are more precise in adjusting their sex allocation appropriately, or both. The perception of social group size is obtained by means of species-specific waterborne chemical cues (Schleicherová et al. 2006). Schleicherová et al. (2010) simulated group-size variations by varying the concentration of the chemical cues that function for group-size assessment. The authors highlighted that *O. diadema* worms responded to as little as 1 % concentration of the chemical cues produced by 400 hermaphrodites living in 60 ml of water, and noticed that these worms did not make precise sex-allocation adjustments at higher concentration ranges.

The ability to estimate the numerosity of conspecifics has also been shown in the polychaete worm *Dinophilus gyrociliatus*. This worm has separate sexes, with a marked sexual dimorphism and a peculiar mating system. Females are about 1 mm long, whereas males are 20 times smaller (dwarf males) with no digestive system and a shorter life-span than females. Eggs are laid in rigid egg-capsules which typically contain large eggs (80 μm) which are destined to produce females and small eggs (40 μm) which are destined to produce males (Charnov 1987) (Fig. 1.3). Males and females mate within the egg-capsules, which means that females mate with their brothers. Within each egg-capsule, sex ratio is female biased, because the large eggs destined to produce females always outnumber the small eggs which produce males. However, as local mate competition theory

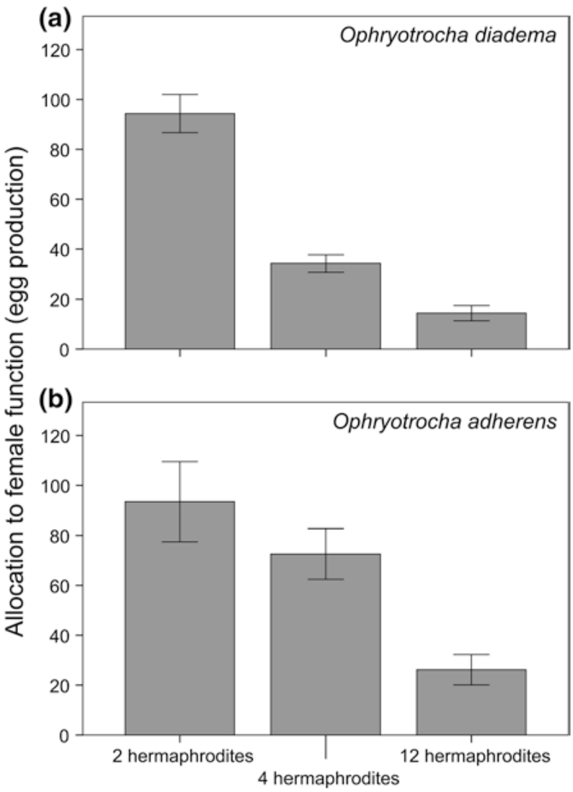


Fig. 1.2 Perception of social group size and variations in the allocation to female function in focal worms in two polychaete species, *Ophryotrocha diadema* and *Ophryotrocha adherens*. **a** *O. diadema* worms responded to differences in group size as small as 2 (group size 2 vs. 4) by altering their female allocation in a highly significant way (GZLM, Poisson distribution, identity link function, Wald $\chi^2 = 302.676$, $P < 0.0001$). They also perceived group size differences between 4 and 12, although allocation adjustments were smaller (Wald $\chi^2 = 118.345$, $P < 0.0001$). **b** *O. adherens* worms had similar responses, but their female allocation adjustments when group size changed from 2 to 4 worms were smaller than when group size changed from 4 to 12 hermaphrodites (2 vs. 4 hermaphrodites: Wald $\chi^2 = 20.025$, $P < 0.0001$; 4 vs. 12 hermaphrodites; Wald $\chi^2 = 158.455$, $P < 0.0001$). Data from (Schleicherová et al. 2014)

(LMC; Hamilton 1967) predicts, mothers are able to adjust their offspring sex-ratio within egg-capsules to the level of mate competition of the patch where they live. As the number of mothers increases in a patch, mothers increase the proportion of sons among their offspring (Minetti et al. 2013). Like hermaphroditic polychaete worms, these worms also estimate the numerosity of worms that are around in the patch but do not use worm density as a cue (Minetti et al. 2013). The adjustment of offspring sex-ratio by the females of *D. gyrociliatus* requires the estimate of the numerosity of worms in the patch.

Fig. 1.3 An egg-capsule of *Dinophilus gyrociliatus* with three large female eggs and a small male egg

Recognizing Relatedness

Annelids can estimate some level of similarity to their conspecifics, such as the relatedness they share with their partners or whether they belong to the same or a different population.

Earthworms have low dispersal ability and some degree of inbreeding may occur in their populations. Experimental evidence suggests that non-selfing hermaphroditic earthworms *E. andrei* adjust breeding effort to mate relatedness. Indeed, when they were forced to mate with siblings, they produced smaller egg cocoons than when they were paired to unrelated partners. In this way they reduced their investment in eggs when the likelihood of producing viable offspring (due to inbreeding depression) was low (Velando et al. 2006).

In the polychaete worm *N. acuminata*, there is evidence that worms changed their behavior when they were exposed to waterborne chemicals produced by conspecifics from other populations, thus demonstrating a role of chemoreception in the discrimination between "home" and allopatric populations (Sutton et al. 2005). This result indicates that *N. acuminata* is able to perform a sort of chemically based "kin" recognition. Similarly, *O. labronica* worms discriminate between conspecifics depending on their population of origin, and preferentially court partners from their own population (Åkesson 1972; Lanfranco and Rolando 1981).

Selective Pressures for Social Recognition in Annelids

Although the number of focused studies is low, there are a few that show that some form of social recognition has emerged in annelids (Table 1.1). In some cases, social recognition may have emerged by natural selection. However, in others, sophisticated cognitive abilities like the assessment of social group size (i.e., numerosity) have emerged because they confer mating advantages. Therefore, they are likely to have evolved via sexual selection. We have been made aware from the time

Table 1.1 Evidence for different kinds of class-level social recognition in Annelids and the type of selection which may have driven them

Species	Type of class-level recognition	Sensory channel	Evidence from experimental tests	References	Selective pressure favoring recognition
Odontosyllis enopla	Mates from non mates	Visual	Field observations	Fischer and Fischer (1996)	Sexual and/or natural selection
Ophryotrocha labronica	Mate quality assessment	Tactile and/or chemical	Male exposure to female-extracts; female preference for large males	Berglund (1990, 1991)	Sexual selection
	Kin recognition	Unknown	Courtship behavior between partners belonging to geographically distant populations.	Åkesson (1972) Lanfranco and Rolando (1981)	Natural selection
Ophryotrocha puerilis	Mates from non mates	Chemical	Males exposure to female-extracts	Berglund (1990, 1991)	Sexual and/or natural selection
	Mate quality assessment	Tactile and/or chemical	Female preferences for small males	Berglund (1990)	Sexual selection
Helobdella papillornata	Group size	Chemical	Increase of the testisac volume in large groups	Tan et al. (2004)	Sexual selection
Ophryotrocha diadema	Group size	Chemical	Female allocation adjustments in response to different mating opportunities	Schleicherová et al. (2006, 2014)	Sexual selection
	Mate quality assessment	Tactile and/or chemical	Hermaphrodites preference for sexually mature partners	Sella (1990)	Sexual selection
Ophryotrocha adherens	Group size	Unknown	Female allocation adjustments in response to different mating opportunities	Schleicherová et al. (2014)	Sexual selection
Ophryotrocha gracilis	Group size	Unknown	Female allocation adjustments in response to different mating opportunities	Schleicherová et al. (2014)	Sexual selection
	Mate quality assessment	Tactile and/or chemical	Hermaphrodites preference for sexually mature partners	Sella et al. (1997)	Sexual selection
Dynophilus gyrociliatus	Group size	Unknown	Females change the offspring sex-ratio in response to variations in population size	Minetti et al. (2013)	Local mate competition

(continued)

Table 1.1 (continued)

Species	Type of class-level recognition	Sensory channel	Evidence from experimental tests	References	Selective pressure favoring recognition
Eisenia fetida	Conspecifics	Tactile	Coordination of collective movements	Zirbes et al. (2010)	Natural selection
	Mate quality assessment	Unknown	Size-related mate choice and ejaculate volume adjustments after assessment of the partner status	Monroy et al. (2005) Velando et al. (2008)	Sexual selection
Eisenia andrei	Mate quality assessment	Unknown	Size-related mate choice and ejaculate volume adjustments after assessment of the partner status	Velando et al. (2008)	Sexual selection
	Kin recognition	Unknown	Reduced cocoon production in pair with a sibling partner	Velando et al. (2006)	Natural selection
Lumbricus terrestris	Mate quality assessment	Tactile or chemical	Size-related mate choice and ejaculate volume adjustments after assessment of the partner status	Domínguez and Velando (2013) Michiels et al. (2001)	Sexual selection
Neanthes acuminata	Male ability to provide paternal care	Chemical	Mate choice for fatherhood experienced males	Fletcher et al. (2009) Storey et al. (2013)	Sexual selection
	Kin recognition	Chemical	Aggressive behavior	Sutton et al. (2005)	Natural selection
Nereis succinea	Mates from non-mates	Chemical	Finding a mate	Ram et al. (2008)	Natural selection

of Darwin that sexual selection has been involved as the form of selection favoring a wide range of traits in males, but we now know that it is also at work in hermaphrodites (Lorenzi and Sella 2008; Anthes 2010; Leonard 2006). However, whether sexual selection has promoted the evolution of cognitive abilities has been rarely investigated. In this short chapter, we have shown that sexual selection is likely to be responsible for the evolution of social group size assessment in hermaphroditic and gonochoric polychaetes, as they respond to group size by varying the proportion of resources they allocate to the male and female function appropriately.

Many animals can discriminate the number of conspecifics in their population or neighbourhood. For example, lionesses adjust their agonistic behaviour to the numerosity of their own group as well as of the opposing group in territorial contests (McComb et al. 1994). Guppies and other fish reduce the risk of predation by aggregating in large groups of conspecifics (shoal). For each fish, predation risk is diluted in larger shoals, and evidence has shown that these fish can discriminate conspecifics' numerosity and prefer joining the larger shoals (Agrillo et al. 2008). In these two examples, the main selective force favouring the ability to discriminate conspecifics' numerosity is natural selection. Natural selection favours lionesses which make precise estimate of their group numerosity relative to that of the opponent group (thus making appropriate decisions on the costs and benefits of aggressive behaviours). Natural selection (through predation pressure) favours guppies which estimate conspecifics' numerosity and join larger shoals. In contrast, in polychaetes, the assessment of numerosity is likely to have evolved by sexual selection, because there are no traits that can be crucially affected by the ability to estimate numerosity other than allocation of resources to male and female function.

Recently, Hollis and Kawecki (2014) have documented that cognitive abilities declined in males of *Drosophila* which were forced to reproduce for more than 100 generations under monogamy. Their cognitive abilities declined more than those of males of polygamous populations that faced both multiple males (i.e., competitors for mating) and multiple females (i.e., mate choice). Potentially, enforced monogamy in simultaneous hermaphrodites could produce similar results after generations, with hermaphrodites reducing their cognitive abilities and losing their ability to estimate group size more than hermaphrodites reared in promiscuity persistently.

References

Agrillo C, Dadda M, Serena G, Bisazza A (2008) Do fish count? Spontaneous discrimination of quantity in female mosquitofish. Anim Cogn 11:495–503

Åkesson B (1972) Incipient reproductive isolation between geographic populations of *Ophryotrocha labronica* (Polychaeta, Dorvilleidae). Zool Scr 1(4):207–210

Anthes N (2010) Mate choice and reproductive conflict in simultaneous hermaphrodites. Animal behaviour: evolution and mechanisms. Springer, New York, pp 329–357

Axelrod R, Hamilton WD (1981) The evolution of cooperation. Science 211(4489):1390–1396

Berglund A (1986) Sex change by a polychaete: effects of social and reproductive costs. Ecology 67(4):836–845

Berglund A (1990) Sequential hermaphroditism and the size-advantage hypothesis: an experimental test. Anim Behav 39(3):426–433

Berglund A (1991) To change or not to change sex: a comparison between two *Ophryotrocha* species (Polychaeta). Evol Ecol 5(2):128–135

Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton

Charnov EL (1987) Local mate competition and sex ratio in the diploid worm *Dinophilus*. Int J Invertebr Reprod Dev 12(2):223–225

Darwin C (1871) The descent of man, and selection in relation to sex. Murray, London

di Bona V, Lorenzi MC, Sella G (2010) Functional males in pair-mating outcrossing hermaphrodites. Biol J Linn Soc 100(2):451–456

Domínguez J, Velando A (2013) Sexual selection in earthworms: Mate choice, sperm competition, differential allocation and partner manipulation. Appl Soil Ecol 69:21–27

Fischer A, Fischer U (1996) On the life-style and life-cycle of the luminescent polychaete *Odontosyllis enopla* (Annelida: Polychaeta). Invertebr Biol:236–247

Fletcher N, Storey EJ, Johnson M, Reish DJ, Hardege JD (2009) Experience matters: females use smell to select experienced males for paternal care. PLoS ONE 4(11):e7672

Gherardi F, Aquiloni L, Tricarico E (2012) Revisiting social recognition systems in invertebrates. Anim Cogn 15(5):745–762

Grothe C, Pfannenstiel H-D (1986) Cytophysiological study of neurosecretory and pheromonal influences on sexual development in *Ophryotrocha puerilis* (Polychaeta, Dorvilleidae). Int J Invertebr Reprod Dev 10(2):227–239

Hamilton WD (1967) Extraordinary sex-ratios. Science 156:477–488

Hardege JD (1999) Nereidid polychaetes as model organisms for marine chemical ecology. Hydrobiologia 402:145–161

Hollis B, Kawecki TJ (2014) Male cognitive performance declines in the absence of sexual selection. Proc Roy Soc B Biol Sci 281(1781):20132873

Lanfranco M, Rolando A (1981) Sexual races and reproductive isolation in *Ophryotrocha labronica* La Greca and Bacci (Annelida, Polychaeta). Ital J Zool 48(3–4):291–294

Leonard JL (2005) Bateman's principle and simultaneous hermaphrodites: a paradox. Integr Comp Biol 45(5):856–873

Leonard JL (2006) Sexual selection: lessons from hermaphrodite mating systems. Integr Comp Biol 46(4):349–367

Lindsay SM (2009) Ecology and biology of chemoreception in polychaetes. Zoosymposia 2:339–367

Lorenzi MC, Sella G (2000) Is individual recognition involved in the maintenance of pair bonds in *Ophryotrocha diadema* (Dorvilleidae Polychaeta)? Ethol Ecol Evol 12(2):197–202

Lorenzi MC, Sella G (2008) A measure of sexual selection in hermaphroditic animals: parentage skew and the opportunity for selection. J Evol Biol 21(3):827–833

Lorenzi MC, Sella G, Schleicherová D, Ramella L (2005) Outcrossing hermaphroditic polychaete worms adjust their sex allocation to social conditions. J Evol Biol 18(5):1341–1347

Lorenzi MC, Schleicherova D, Sella G (2008) Sex adjustments are not functionally costly in simultaneous hermaphrodites. Mar Biol 153(4):599–604

Lorenzi MC, Schleicherová D, Sella G (2014) Multiple paternity and mate competition in nonselfing, monogamous, egg-trading hermaphrodites. Acta Ethologica 17:173–179

McComb K, Packer C, Pusey A (1994) Roaring and numerical assessment in contests between groups of female lions. Panthera leo Anim Behav 47:379–387

Michiels NK, Hohner A, Vorndran IC (2001) Precopulatory mate assessment in relation to body size in the earthworm *Lumbricus terrestris*: avoidance of dangerous liaisons? Behav Ecol 12(5):612–618

Minetti C, Sella G, Lorenzi MC (2013) Population size, not density, serves as a cue for sex ratio adjustments in polychaete worms. Ital J Zool 80(4):547–551

Monroy F, Aira M, Velando A, Domínguez J (2003) Have spermatophores in *Eisenia fetida* (Oligochaeta, Lumbricidae) any reproductive role? The 7th international symposium on earthworm ecology, Cardiff, Wales. Pedobiologia 47(5):526–529

Monroy F, Aira M, Velando A, Domínguez J (2005) Size-assortative mating in the earthworm *Eisenia fetida* (Oligochaeta, Lumbricidae). J Ethol 23(1):69–70

Parker G (1998) Sperm competition and the evolution of ejaculates: towards a theory base. In: Tim RB, Anders PM (eds) Sperm competition and sexual selection. Academic Press, New York, pp 3–54

Purschke G (2005) Sense organs in polychaetes (Annelida). Morphology, molecules, evolution and phylogeny in polychaeta and related taxa. Springer, New York, pp 53–78

Ram JL, Fei X, Danaher SM, Lu S, Breithaupt T, Hardege JD (2008) Finding females: pheromone-guided reproductive tracking behavior by male *Nereis succinea* in the marine environment. J Exp Biol 211(5):757–765

Salva OR, Regolin L, Mascalzoni E, Vallortigara G (2012) Cerebral and behavioural asymmetries in animal social recognition. Comp Cogn Behav Rev 7:110–138

Schleicherová D, Lorenzi MC, Sella G (2006) How outcrossing hermaphrodites sense the presence of conspecifics and suppress female allocation. Behav Ecol 17(1):1–5

Schleicherová D, Lorenzi MC, Sella G, Michiels N (2010) Gender expression and group size: a test in a hermaphroditic and a gonochoric congeneric species of *Ophryotrocha* (Polychaeta). J Exp Biol 213(9):1586–1590

Schleicherová D, Sella G, Meconcelli S, Simonini R, Martino M, Cervella P, Lorenzi MC (2014) Does the cost of a function affect its degree of plasticity? A test on plastic sex allocation in three closely related species of hermaphrodites. J Exp Mar Biol Ecol 453:148–153

Schärer L (2009) Tests of sex allocation theory in simultaneously hermaphroditic animals. Evolution 63(6):1377–1405

Sella G (1985) Reciprocal egg trading and brood care in a hermaphroditic polychaete worm. Anim Behav 33(3):938–944

Sella G (1988) Reciprocation, reproductive success, and safeguards against cheating in a hermaphroditic polychaete worm, *Ophryotrocha diadema* Åkesson, 1976. Biol Bull 175(2):212–217

Sella G (1990) Sex allocation in the simultaneously hermaphroditic polychaete worm *Ophryotrocha diadema*. Ecology 71(1):27–32

Sella G (2006) Sexual strategies and mating systems. In: Rouse G, Pleijel F (eds) Reproductive biology and phylogeny in Annelida. Science Publishers, Enfield, pp 77–92

Sella G, Premoli MC, Turri F (1997) Egg trading in the simultaneously hermaphroditic polychaete worm *Ophryotrocha gracilis* (Huth). Behav Ecol 8:83–86

Sherman PW, Reeve HK, Pfennig DW (1997) Recognition systems. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell Science, Oxford, pp 69–96

Simonini R, Massamba-N'siala G, Grandi V, Prevedelli D (2009) Distribution of the genus *Ophryotrocha* (Polychaeta) in Italy: new records and comments on the biogeography of Mediterranean species. Vie et Milieu 59(1):79–88

Storey EJ, Reish DJ, Hardege JD (2013) Conditioned water affects pair formation behaviour in the marine polychaete *Neanthes (Nereis) acuminata*. Anim Cogn 16(1):85–89

Sutton R, Bolton E, Bartels-Hardege H, Eswards M, Reish D, Hardege JD (2005) Chemical signal mediated premating reproductive isolation in a marine polychaete, *Neanthes acuminata (arenaceodentata)*. J Chem Ecol 31(8):1865–1876

Tan G, Govedich F, Burd M (2004) Social group size, potential sperm competition and reproductive investment in a hermaphroditic leech, *Helobdella papillornata* (Euhirudinea: Glossiphoniidae). J Evol Biol 17(3):574–580

Tibbetts EA, Dale J (2007) Individual recognition: it is good to be different. Trends Ecol Evol 22(10):529–537

Velando A, Domínguez J, Ferreiro A (2006) Inbreeding and outbreeding reduces cocoon production in the earthworm *Eisenia andrei*. Eur J Soil Biol 42:S354–S357

Velando A, Eiroa J, Domínguez J (2008) Brainless but not clueless: earthworms boost their ejaculates when they detect fecund non-virgin partners. Proc Roy Soc B Biol Sci 275(1638):1067–1072

Wald G, Rayport S (1977) Vision in annelid worms. Science 196(4297):1434–1439

Watson G, Bentley M, Gaudron S, Hardege JD (2003) The role of chemical signals in the spawning induction of polychaete worms and other marine invertebrates. J Exp Mar Biol Ecol 294(2):169–187

Wedell N, Gage MJ, Parker GA (2002) Sperm competition, male prudence and sperm-limited females. Trends Ecol Evol 17(7):313–320

Wolken JJ, Florida RG (1984) The eye structure of the bioluminescent fireworm of Bermuda, *Odontosyllis enopla*. Biol Bull 166(1):260–268

Zimmer RK, Butman CA (2000) Chemical signaling processes in the marine environment. Biol Bull 198(2):168–187

Zirbes L, Deneubourg JL, Brostaux Y, Haubruge E (2010) A new case of consensual decision: collective movement in earthworms. Ethology 116(6):546–553

Chapter 2
Individual Recognition in Stomatopods

Kristina Mead Vetter and Roy L. Caldwell

Abstract Many stomatopod species seem capable of individual recognition. This ability appears most often in species that face severe competition for shelter, or that create shelters that are costly to reproduce. Mantis shrimp identify specific individuals (conspecific or otherwise), and adapt their defensive or offensive strategies in response to previous encounters with that opponent. Stomatopods also use individual recognition in reproductive contexts: to recognize current mates and young, and to avoid previous mates. Current thinking is that individual recognition serves to limit lethal aggression, always a risk due to the legendary strikes of their powerful raptorial appendages. The most aggressive species, with the most complex behavioral repertoires, appear to be most capable in this arena. This chapter describes the well-developed visual and chemical senses and the learning that supports this survival strategy, and then focuses on the evidence supporting chemically-mediated individual recognition. This is followed by accounts of the roles played by visual and auditory cues in individual recognition.

Introduction

Basic Stomatopod Biology

Members of the order Stomatopoda, also known as mantis shrimp, are the only living order of the subclass Hoplocarida. Stomatopods are marine carnivorous malacostracan crustaceans that mostly live in tropical or subtropical oceans, although a few temperate

---

K.M. Vetter (✉)
Department of Biology, Ohlone College, Fremont, California 94539, USA
e-mail: ksmvetter@gmail.com

R.L. Caldwell
Department of Integrative Biology, University of California, Berkeley,
California 94303, USA
e-mail: rlcaldwell@berkeley.edu

L. Aquiloni and E. Tricarico (eds.), *Social Recognition in Invertebrates*,
DOI 10.1007/978-3-319-17599-7_2

species are known. Species of mantis shrimp typically obtain a maximum body length of 2–35 cm. Identifying features include specialized stalked eyes, tripartite antennules that are highly sensitive to a variety of odors, and raptorial appendages capable of very rapid and powerful strikes. Compared to many other crustaceans, mantis shrimp exhibit complex aggressive behaviors. They also are capable of relatively sophisticated learning. These traits set the stage for the development of individual recognition.

The Importance of Shelter and Raptorial Appendage Type

With few exceptions, most adult mantis shrimp spend much of their time in some kind of shelter. They often lurk at the entrance, and emerge to hunt prey with startling swiftness. Their raptorial appendages (enlarged second thoracopods) are typically either long, spiny spearing appendages, or hardened smashing appendages with enlarged muscle mass, although other forms exist (Schram et al. 2013). The designation as "smasher" or "spearer" refers to the mode of hunting prey, but these categories also often relate to broad differences in habitat, anatomy, and behavior (Mead and Caldwell 2011). Families with spearing raptorial appendages include Bathysquillidae, Erythrosquillidae, Eurysquillidae, Indosquillidae, Lysiosquillidea, Nannosquillidae, Parasquilloidea, Squilloidea, and Tetrasquillidae. Smashers include the Corononididae, Gonodactylidae, Odontodactylidae, Protosquillidae, and Takuidae. There are, of course, exceptions to this division, as detailed in Schram et al. (2013), and some groups, especially among the Squillidae, have not been studied sufficiently to determine if their life style deviates from these patterns.

Stomatopod species vary greatly in the type of refuge occupied, the time and effort required to secure a home, and in their vulnerability to predation when they leave their shelter. The type of refuge preferred is strongly, but not perfectly, correlated with their raptorial appendage (Caldwell and Dingle 1975, 1976). Most spearing species excavate burrows in soft substrata (Fig. 2.1a), while most smashing species occupy cavities in coral rubble (Fig. 2.1b) or other hard substrata. Pseudosquillidae, spearers that group functionally with smashers¸ start their post-settlement life in coral or coral rubble and thus face many of the same constraints as smashers. Burrows or cavities are critical for many aspects of mantis shrimp ecology. They provide shelter from predators, a location for processing prey, and a safe haven for mating and for the guarding of eggs and larvae. Species that live in preexisting cavities in hard substrata such as coral, rather than burrows that they excavate themselves, often face strong competition for these cavities. This competition is intense due to defensive needs and reproductive constraints. Effective defense requires that the entrance diameter match the body diameter. Since stomatopods have indeterminate growth, they must modify or exchange their shelters after each molt. Species living in sand or mud can usually expand their burrows without abandoning them, but species living in rock or coral cavities cannot easily enlarge their dwellings and must often fight the current inhabitant to take control of a new, larger cavity. Furthermore, in non-monogamous species, the animals often face eviction from burrows during mating periods. In many species, the males, females, or both

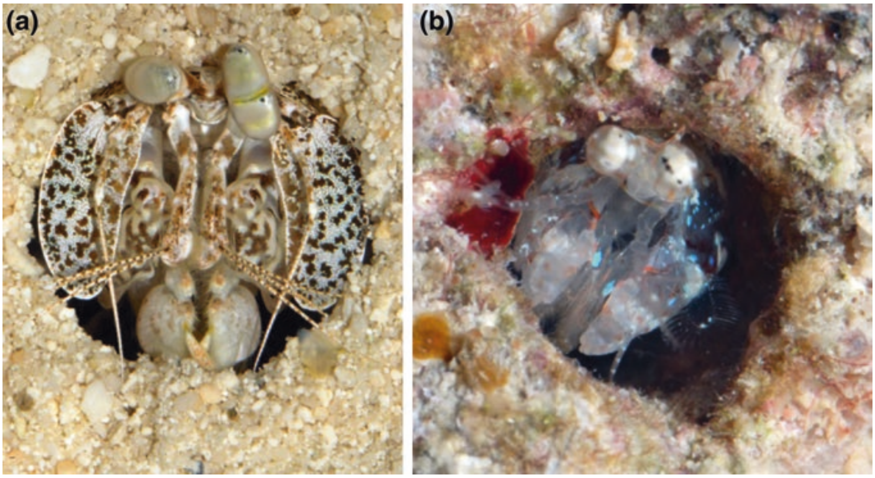


Fig. 2.1 Stomatopod shelters. **a** *Lysiosquilla maculata* in burrow in consolidated sand. **b** *Gonodactylus affinis* in coral cavity

leave their shelter as often as every lunar cycle to search for a mate (Caldwell 1991). The scenario is especially grim for a male: he leaves his cavity to search for a mate, risking that it will be occupied during his absence. If he finds a mate and guards her in her burrow, he must still leave once she lays her egg mass, and hunt for a new cavity. Either the resident mating partner is evicted, or the visitor returns to find its burrow occupied and must fight for it. This frequent exposure to predation and to competition over cavities exerts a heavy toll (Caldwell 1991).

Coral-dwelling mantis shrimp face limited availability of crevices suitable for shelter. Large cavities are scarcer than small ones (Reaka and Manning 1981). This situation leads to increased aggression with an increase in body size, both within and among species (Reaka and Manning 1981). For example, the largest cavity-living Costa Rican stomatopod, *Gonodactylus festae*, shows the most intense aggression, and has the highest incidence of wounds of the five species studied (Reaka and Manning 1980).

Even though the smashing species usually face greater competition for suitable cavities than spearers, both groups experience aggression, and animals with either type of raptorial appendages are capable of dealing lethal blues to conspecifics as well as to prey.

This fierce competition for burrow space, combined with the potentially lethal weapons at their disposal, places a premium on rapid, accurate information that can reduce the risk involved in assessing and fighting other stomatopods and other dangerous competitors. As a consequence, the visual and olfactory systems of stomatopods, particularly smashing species living in hard cavities, are very well developed. Complex behaviors, involving displays, assessment of aggression, learning, and individual recognition are well established. These features of stomatopod biology serve to mitigate the risk that competitive encounters will become lethal.

Patterns of Individual Recognition in Mantis Shrimp

Although this book is on the wider topic of social recognition, this chapter focuses on the subset of interactions governed by individual recognition. Individual recognition is defined here as the ability to identify and remember (at least for a period of time) specific individuals, based on previous experience. The idea, as expressed in Caldwell (1985), is that animals "use knowledge of their opponents gained during previous encounters [to choose] the aggressive strategies and tactics to be employed during subsequent interactions." This is in contrast to some forms of social recognition, where identification is to group, such as members of a species, males versus females, previously encountered animals versus strangers, or juveniles versus sexually mature animals, rather than to a specific individual.

Individual recognition in stomatopods was first studied in the context of aggressive interactions, specifically in regards to contests over shelter. This focus still represents the majority of the studies of individual recognition in mantis shrimp, but subsequent research has included the roles of individual recognition in reproduction. Here, too, the threat of violence is ever present, since a potential mate could also be a combatant.

It should be noted, however, that there is a continuum between social recognition (i.e., members of a group) and individual recognition. Individual recognition occurs when animals classify other creatures by a sufficient number of criteria so that the probability of confounding one individual with another becomes vanishingly small. What constitutes sufficient criteria will most likely vary with the type of sensory cues being used, the precision of the signal and the acuity of the receptor, the number of individuals that must be distinguished, and a variety of other factors that we can only guess at, especially since we do not know the exact natures of the cues involved. Given their sensory acuity and the large number of available cues, it is likely that most or all stomatopods practice at least some form of social recognition. For example, all mantis shrimp can probably recognize conspecifics and sex. In some, as described below, this ability has been honed to the level of identifying and remembering specific individuals.

Individual recognition occurs in a subset of mantis shrimp species (Table 2.1), and plays a variety of different roles, although many of them are related to the

Table 2.1 Individual recognition in mantis shrimp families

Superfamily and family	Raptorial appendage	Habitat and burrow	Contact, mating	Aggression	Individual recognition
Bathysquilloidea					
Bathysquillidae	Spearer	Burrow in mud, sand	Mate search	Low	Probably not
Indosquillidae	Spearer	Burrow in mud, sand	Mate search	Low	Probably not
Erythrosquilloidea					
Erythrosquillidae	Spearer	Burrow in mud, sand	Mate search	Low	Probably not

(continued)

Table 2.1 (continued)

Superfamily and family	Raptorial appendage	Habitat and burrow	Contact, mating	Aggression	Individual recognition
Eurysquilloidea					
Eurysquillidae	Spearer	Burrow in mud, sand	Mate search	Low	Probably not
Gonodactyloidea					
Alainosquillidae	Smasher	Cavity in rock, coral	Many new partners	Moderate	Unknown
Gonodactylidae	Smasher	Cavity in rock, coral	Frequent contact	Very high	Yes, odor
Hemisquillidae	Blunt[a]	Burrow in firm sand	Some contact	Can be high	Probably
Odontodactylidae	Smasher	Burrow in sand, gravel	Many new partners	Moderate	Probably
Protosquillidae	Smasher	Cavity in rock, coral	Mate guard	High	Yes, visual cues
Pseudosquillidae	Spearer[b]	Cavity or burrow	Many new partners	High	Yes, odor and visual?
Takuidae	Smasher	Cavity in rock, coral	Mate guard	High	Unknown
Lysiosquilloidea					
Coronididae	Smasher	Cavity in rock		Low	Unknown
Lysiosquillidae	Spearer	Extensive burrow[c]	Mono-gamy	Low	Yes
Nannosquillidae	Spearer	Extensive burrow[c]	Some in pairs	Low	Probably
Tetrasquillidae	Spearer	Extensive burrow[c]	May pair	Low	Probably
Parasquilloidea					
Parasquillidae	Spearer	Burrow in mud, sand	Mate search	Low	Probably not
Squilloidea					
Squillidae	Spearer	Burrow in mud, sand	Some guarding[d]	Low	Likely in *Meiosquilla*

Columns are explained as follows: Many features of a group's ecology and behavior correlate with the type of raptorial appendage. Species that find refuge in preexisting cavities or that create extensive burrows are more likely to have some form of individual or social recognition. Species that come into frequent contact with a limited number of individuals on a long-term basis, engage in monogamy or mate-guarding, or are more aggressive, are more likely to use individual recognition. Some characteristics show too much variability within a family to describe. *Notes* [a]The Hemisquillidae possess raptorial appendages that are blunt, and fit neither the smasher nor the spearer category. They may be basal. [b]While morphologically a spearer, with two spines, the Pseudosquillidae are often grouped with the smashers because of habitat and behavioral reasons. [c]These burrows in sand and rubble are extensive and mucus-lined, and thus very expensive to build. [d]*Meiosquilla* is thought to have a mating system similar to that of *N. bredini*. Information for this table comes from Caldwell (1991), Caldwell and Dingle (1975), Reaka and Manning (1981), Schram et al. (2013)

need to modulate aggression. There are several conditions that must be met, before individual recognition is likely to be established. First, there must be variation in individual presentation, via the sensory modality utilized (visual, chemical, audio cues, or a combination thereof). Second, the sensory apparatus must be sufficiently sophisticated to detect individual differences. Third, there must be an element of learning and memory so that the initial encounter is remembered and can affect subsequent meetings. Lastly, (at least for us to recognize the event!) the animal must have a flexible behavioral repertoire, so that distinct behavioral outcomes can result from the encounter and recognition of different particular individuals.

As will be described below, smashers generally have more sophisticated visual senses than spearers (except for pseudosquillids). Smashers often live in clear, well-lit habitats, and make the most of these signaling opportunities. The stomatopod families exhibiting the greatest aggression, behavioral complexity and flexibility are the Gonodactylidae, Protosquillidae, Takuidae, Odontodactylidae (all smashers), and Pseudosquillidae (functionally grouped with smashers). We can thus expect a greater reliance on individual recognition among these groups (Table 2.1), although there are exceptions.

Learning and Memory in Mantis Shrimp

Learning is an important part of the visual, olfactory, and vibrational communication between mates, competitors, and even among species (Cronin et al. 2006), and is essential to the rapid decision making attending courtship and mating. The facility with which mantis shrimp learn accurately and quickly is probably a product of numerous factors, including the probability of damage from aggressive contests, predation pressure, the strong need and capacity for behavioral flexibility, the complexity of their visual system, and the ecology of their environment (Cronin et al. 2006). Mantis shrimp are one of the few animals able to disable or kill a conspecific opponent with a single strike of their raptorial appendages. Use of such a fearsome appendage requires care, especially since a misaimed or poorly timed blow can damage the perpetrator. Since the attacker itself is vulnerable, it must be able to size up opponents and make quick decisions about whether or not to engage (Cronin et al. 2006). This careful, but rapid evaluation is especially important since an animal that is a prospective mate one day may be an unwelcome intruder on the next day. Given that the smashers generally have the most complicated behavior and probably benefit the most from behavioral flexibility, learning is probably most developed in these groups (Cronin et al. 2006).

Social conditions are also important, because there is a finite limit to how many other animals an individual can "remember", or the time over which this learning persists. For instance, if a mantis shrimp lives in a solitary manner, or if it encounters many tens of individuals a day with no repeats, then individual recognition is unlikely to play a pivotal role for that animal. In contrast, social and environmental factors leading to repeat interactions increase the likelihood of individual recognition playing a role. Examples include multiple Neogonodactylids occupying individual cavities in the same rock, or a monogamous pair of *Lysiosquillina* inhabiting the same burrow. R. L. Caldwell (*pers. obs*) has seen up to 22 *Neogonodactylus bredini* inhabiting cavities in the same rock over at least several consecutive days. By comparison, *Hemisquilla californiensis* and *Squilla empusa* live at a much lower density, with distances on the order of meters separating their burrows in the sand and mud (Reaka and Manning 1981; Staaterman et al. 2011; Mead and Minshall 2012). The lower concentration of shelters and the less stringent competition for space may imply fewer aggressive encounters with other individuals. However, at least some *H. californiensis* routinely forage tens of meters away from their burrows (Caldwell, *pers. obs.*) and thus have a greater change of encountering conspecifics, so this calculus is not clear.

The moderate permanence exhibited by the *N. bredini* sharing a rock is probably another requirement for individual recognition. In the laboratory, the behavioral changes that indicate individual recognition seem to persist about four weeks after the initial exposure (Caldwell 1991). In *N. bredini*, at least, this timing correlates with their reproductive periodicity: female receptivity and male-female pairing is timed with the full moon, and brooding lasts nearly the whole of the following month. Although it hasn't been formally tested, the permanence of the individual recognition is likely to vary with mating pattern. *Lysiosquillina,* for example, pair for decades. If separated after several years of sharing a burrow, the recognition would be predicted to continue for much longer than in *N. bredini*.

Behavioral Complexity and Flexibility

One of the hallmarks of the Stomatopoda is their complex array of behaviors, especially regarding aggressive contests over habitat and mating rituals. The behaviors are simultaneously complex and flexible, enabling them to adapt to the particular social and environmental context of the current manifestation of the behavior. This flexibility is relevant to individual recognition, because it enables them to respond differently to different individuals and context combinations. This plasticity of response is probably due in part to the incredible "dexterity" of their appendages, especially their maxillipeds. These appendages allow for an almost infinite variety of behaviors involved in grooming, burrow excavation and maintenance, current production, food searching and manipulation, displays, courtship, egg mass handling, and other essential functions.

Other appendages used in signaling displays include the antennules, antennal scales, and the raptorial appendages. One common behavioral display with a variety of functions is the meral spread. In this posture, all maxillipeds, antennules, and antennule scales are extended laterally and held statically. Meral spreads can play at least three roles including antipredator defense, intraspecific defense (such as cavity defense), and courtship. The extent and intent of the meral spread varies among groups. The antipredator meral spread, shown by all stomatopods, tends to be the most dramatic. Meral spreads used during conspecific fights are smaller and are directed specifically at the opponent. Meral spreads used during courtship tend to include maxilliped whirling, which probably acts to conduct chemical information as well as serving as an additional facet of the display (Caldwell and Dingle 1976). Because these displays are used as a measure of aggressiveness, their mode of use in an animal's behavior during an encounter is an important indicator of recognition. Other aspects of the meral spread, especially the meral spots on the raptorial appendages, may be important in species recognition, territoriality, and other aspects of social recognition (Caldwell and Dingle 1975). For example, nearly all stomatopods exhibit the same color of meral spots in males and females of a species (*Neogonodactylus oerstedii* is an exception), and different species tend to have different color spots.

Additional factors leading to behavioral flexibility include the fine sensory acuity experienced by many mantis shrimp, and of course the constant threat of damage if signals are misinterpreted.

While most mantis shrimp are inquisitive and adept at manipulating their environment, the pattern differentiating smashers and spearers is evident. Smashers consistently show more complex types of agonistic interactions than spearers. For example, smashers show 12–15 different categories of acts, with more frequent displays, while spearers show 6–10 categories of acts, with less frequent displays (Caldwell and Dingle 1975).

The next section of this chapter deals with individual recognition using chemical cues, which is the best-studied form of individual recognition among mantis shrimp. This will be followed by a brief treatment of the role of visual cues in individual recognition, and a short section on the potential for individual recognition using audial cues among mantis shrimp. We will then discuss multimodality and the dominant role of chemical cues.

Individual Recognition Using Chemical Cues

Chemical Senses and Olfactory Apparatus

Chemical sensing can be separated into olfaction ("smell") and distributed chemoreception (Schmidt and Mellon 2011). Olfaction tends to refer to a distant source, while the distributed chemoreceptive sensilla are in physical contact with the stimulus, but the functions can overlap.

Any chemical component to individual recognition is likely to rely on odors from distant sources, and thus would be considered an aspect of olfaction. Ablation experiments suggest that the portions of the mantis shrimp olfactory apparatus responsible for individual recognition are the unimodal chemosensory sensilla (aesthetascs) located on their antennules (Fig. 2.2a) (Mead and Caldwell 2011). These aethetascs are located on the distal portion of the dorsolateral flagellum (Fig. 2.2b) (Hallberg et al. 1992; Mead and Weatherby 2002; Derby et al. 2003). Aesthetascs are long, slender, thinly cuticularized structures inserted into the flagellum at an angle of 40–60° in rows of three (Mead et al. 1999; Mead and

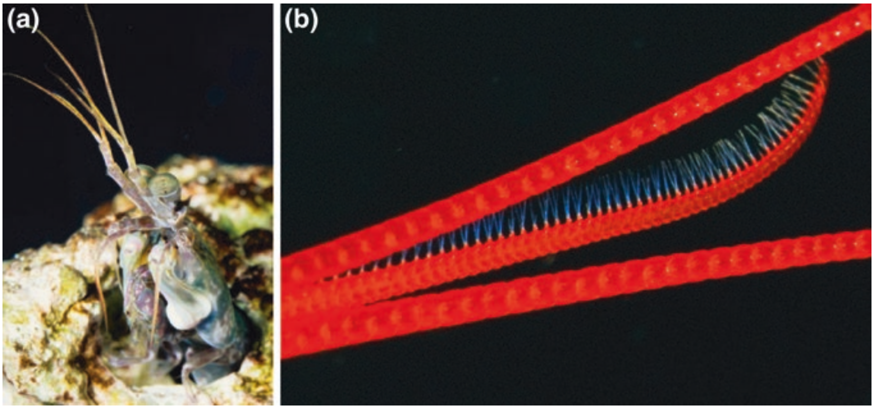


Fig. 2.2 Olfaction. **a** Antennules from *Haptosquilla bangai.* **b** Close-up of an antennule from a male *Odontodactylus scyllarus*, showing aesthetascs

Weatherby 2002). Their length and diameter depend on size and species, varying from 10 µm in diameter and 200 µm length in an 8 mm telson-rostrum length *Gonodactylaceus falcatus* to 32 µm in diameter and 550 µm length in a 157 mm telson-rostrum length *H. californiensis* (Mead and Caldwell 2011). They are innervated by bipolar olfactory receptor neurons (ORNs); there are 12–20 ORNs per aesthetasc in *G. falcatus* (Mead and Weatherby 2002). These chemosensory neurons project proximally to the ipsilateral olfactory lobe, which is organized into spherical glomeruli (Derby et al. 2003).

Chemically Mediated Individual Recognition

Mantis shrimp use chemically mediated individual recognition in a variety of circumstances, including contests over burrows, and in various reproductive behaviors. In no case is the identity of the chemical cues is known, or is the exact mode of delivery. However, there are some likely candidates. When *Haptosquilla* females defend their burrows, they position their telson in the entrance of the cavity and fan their pleopods to push jets of water out of the entrance. Caldwell (*pers. obs.*) has seen fecal pellets included in these jets. *S. empusa* also create currents using their pleopods when disturbed (Mead and Minshall 2012), but no fecal material was observed in this species. Dye studies indicated that female *N. bredini* defending their cavities against approaching males generated currents by whirling their maxillipeds (Caldwell 1992). These currents are thought to carry chemical cues, perhaps in the form of urine as in crayfish (Breithaupt 2001) and lobsters (Aggio and Derby 2011).

Individual Recognition in Aggressive Contests Over Burrows

The first experiments investigating individual recognition in stomatopods were performed using paired aggressive contests over artificial shelter cavities, in the small tropical mantis shrimp species *Neogonodactylus festae.* In the initial study, Caldwell (1979) placed *N. festae* into artificial cavities. After fifteen minutes, a second stomatopod matched for size and sex was introduced into the test arena. The resident and intruder fought for ownership of the cavity, with the resident almost always winning due to positional advantage. The fight was stopped once dominance was established (usually within five minutes). Fifteen minutes later, the intruder was replaced in the test apparatus, which had been cleaned and refilled with seawater, with an artificial cavity that had been filled with one of three types of water. The three test fluids were: "clean" water that had never contained a stomatopod, "stranger" water from the container of a stomatopod of the same size and sex that the intruder had never encountered, or "known victorious resident" water taken from the previously victorious resident's container removed prior to the encounter between them. This testing procedure was repeated over three days, each intruder encountering all three odors, with a randomized order of presentation. While intruders all quickly approached the empty cavities, their behavior was markedly different depending on the source of the water. If there was no odor of another stomatopod, the intruders took no defensive action and entered the cavity within a minute or two. If the cavity contained the odor of another stomatopod with which the intruder had no experience, the intruders entered cautiously, often inserting their armored telson into the entrance as if expecting an attack from the phantom resident. If the cavity contained the odor of the previously encountered resident that had defeated the intruder earlier, most approached the entrance, sampled the odor diffusing from the cavity with their antennules, and immediately fled the area. When exposed to the water containing the odor of a stranger, 50 % entered within 4 min, and all entered by 13 min. However, only 41 % ever entered the cavity containing the odor of the animal that had previously defeated them during the course of the 15 min test.

This experiment opened a new avenue of research for Caldwell and colleagues, but there were some concerns that the results represented intruders responding differently to broader classes of animals such as "known" versus "unknown" opponents, rather than recognizing individuals. To test for this possibility, a different design was needed where the intruder encountered at least two opponents over a short period of time and then reacted differently to them. In this new scenario (Caldwell 1985), intruders were first matched against either a resident that was 5 % longer and could successfully defend its cavity or against a 20 % shorter resident that the intruder could evict. Thirty minutes later, the intruder was matched against the other type of resident. The residents were the same sex as the intruder and the order of presentation was randomized. Thirty minutes later, the intruder was tested using the odor of one of the residents it had just fought and 30 min after that it was tested against the odor of the other resident. The results of these rematches were that intruders quickly entered cavities spiked with the odor of an animal that they had evicted (median time = 19 s), but delayed entering cavities with odor from animals that had successfully defended the cavity in an earlier bout (median time = 324 s; Caldwell 1985). Since the same intruders failed to respond differentially to odors of larger and smaller unfamiliar conspecifics, it is unlikely that odors providing information on size alone served as the basis for the difference in time to enter the cavity. The response to odor was based on previous experience, suggesting individual recognition.

In addition to conspecific individual recognition, experiments with the stomatopod species *Neogonodactylus zacae* and *N. bahiahondensis* suggest that mantis shrimp are able to use chemical cues to discriminate between different individuals of sympatric species as well (Caldwell 1982). In the competition for cavities, what is important is the fighting ability of resident, not its species.

Chemically mediated recognition can even occur across distantly related species that compete for cavities. *N. bredini* and the octopus *Octopus joubini* fight viciously over quality living quarters. *N. bredini* previously exposed to *O. joubini* show greater delay when approaching test cavities containing octopus odor than odor-free cavities (Caldwell and Lamp 1981). Naïve *N. bredini* do not show this response. There is no evidence that the stomatopods are recognizing individual octopus, so this appears to be a form of social recognition rather than individual recognition.

Chemically Mediated Individual Recognition and Reproduction

Since cavities and burrows are as essential for reproduction as for shelter from predation, the potential for aggressive contests over mating space and mating partners is high. Reproductive pressure can add impetus to the already strong impulse to defend space. One can imagine the extra selective pressure to develop individual recognition and thus avoid unnecessary damage.

Individual recognition can have different purposes, depending on the reproductive mode of the species. Mating systems range from life-long monogamy in some lysiosquillids to multiple sequential matings in many neogonodactylids to rampant promiscuity in *Pseudosquilla ciliata* (Caldwell 1987). The following examples detail species with three different mating habits. In each case, the role of individual recognition via odor seems critical, but for different reasons.

All known species of *Lysiosquillina* are spearers that make large (up to 10 m) burrows in soft sediment (Christy and Salmon 1991). Adults are nearly always found in pairs. They have reduced armor and are thus very vulnerable outside of their burrow. Although there is typically plenty of the sandy substrate preferred for excavating burrows, so that there is little of the competition for space experienced by gonodactylids, burrow construction represents a large investment. One of the most costly components is the considerable amount of mucus required to stabilize the burrow walls. The biological cost of the mucus prevents adult *L. sulcata* from being able to construct a new burrow if evicted from their old one (Caldwell 1991). Together, the large investment in burrow construction and the vulnerability to predation are thought to have led to long-term monogamy (Christy and Salmon 1991). Their nocturnal nature, coupled with their dull body color, greater turbidity, and lower light levels of their preferred habitats may have created an additional evolutionary pressure for individual recognition mediated by chemical cues. The use of chemical cues to support mate recognition and monogamy is often seen in crustaceans (e.g. *Hymenocera picta*, Wickler 1973; Wickler and Seibt 1981). Thus, in *Lysiosquillina*, individual recognition facilitates the pair bond.

Individual chemical recognition acts to facilitate reproduction in the opposite way in *P. ciliata,* widely distributed stomatopods found in a variety of habitats. Females will copulate at any stage in their reproductive cycle and have been observed to mate with several different males in one day. Females are extremely aggressive when pursuing mates, often harassing males until they copulate. Mating occurs in the open and the participants separate immediately after coupling. Interestingly, animals that have mated with each other will not remate within the same pair for several hours but they will copulate with a new partner within a few minutes (Hatziolos and Caldwell 1983). This reluctance to pair with a previous mate may be because males are thought to be sperm-limited, and a single copulation is sufficient to fertilize a brood of eggs (Hatziolos and Caldwell 1983). It appears that some form of individual recognition is occurring, this time to avoid the original mate.

Individual chemical recognition plays a different role in *N. bredini.* In this species, males and females are solitary and defend their own cavities except for when they are reproductively active (Shuster and Caldwell 1989). A few days before each full moon, mating pairs form in cavities, which the males guard (Caldwell 1991). Once the female spawns, the male leaves. Caldwell (1992) studied twenty-five mated pairs that produced egg masses. Fourteen days after the male left the breeding cavity, Caldwell (1992) compared the interaction between the female (placed in a new cavity) to the original male and to a stranger male. The males were also tested as intruders against brooding females that they had not previously encountered. Aggressive acts (meral spread threat, lunge, strike; see Caldwell 1979 for precise definition) occurred only 12 % of the time when the original male was introduced to his brooding mate, but 76 % of the time when a stranger male was introduced. Contests between animals that had not previously been paired escalated more rapidly. The reduced aggression displayed by previously paired males was not due to a general holding back in the presence of brooding females or eggs: they attempted to evict "stranger" brooding females. Also, males did not escalate contests when encountering former mates whose eggs had been removed, perhaps because she could be storing his sperm. Thus individual recognition keeps a male from threatening his own current or future offspring (Caldwell 1992).

Other species that experience competition for cavities, high search costs, and guarding of females by males, such as other neogonodactylids and the squillid *Meiosquilla*, are thought to have similar mating systems, and thus perhaps may also rely on individual recognition to modulate aggression.

In an interesting twist, *N. bredini* are able to distinguish males from females by odor, but can't decode the reproductive status of females (Caldwell 1986a).

The females use this to their advantage. Females with ripe ovaries not currently in a pair may go looking for a male. If the moon is full, the male usually admits the female without hesitation. She evicts the male 15 % of the time if she is reproductive, but 33 % of the time if she is non-reproductive (Caldwell 1986a). The males appear to be trading their cavity for the chance to mate. By broadcasting her sex but not signaling her reproductive status, a female increases her overall chances (i.e. not just when she is receptive, but throughout her reproductive cycle) of gaining access to a cavity.

To summarize, individual recognition may serve to promote a variety of functions, but appears to be most common in species that experience high competition for burrows, have costly burrows, or rely on individual recognition to promote reproduction, either by maintaining pair bonding, by facilitating the identification of new partners, or by protecting a reproductive investment.

The Role of Visual Cues in Individual Recognition

Visual System

Mantis shrimp possess appositional compound eyes segmented into three lobes consisting of two peripheral hemispheres separated by a midband of specialized ommatidia (Marshall and Land 1993). This arrangement enables each eye to act as an independent, trinocular rangefinder, since the stomatopod can image the same location in space with three spatially separate areas of the eye (Marshall 1988). They possess a diverse and complex array of photoreceptors capable of perceiving light intensity, color, and polarization (Marshall et al. 2007). They have at least 16 types of visual pigments that are sensitive to wavelengths of light from UV to the near infrared (Marshall et al. 2007). The opsins that respond to UV in *N. oerstedii* appear to interact with four optical filters that extend and diversify the wavelengths to which the animal can respond (Bok et al. 2014). Because the receptors that mediate color vision are arranged linearly, stomatopods have to scan objects of interest (Cronin et al. 2006). Recent discoveries suggest that mantis shrimp use a novel temporal scanning pattern across the photoreceptors, rather than using the color channels comparatively, as in humans and many other animals (Thoen et al. 2014). This approach may allow for particularly rapid decision-making based on visual input, facilitating behavioral flexibility.

An abundance of visual pigments is probably very useful in underwater environments, which tend to be low contrast (Cronin et al. 2006). Even if the original function was probably related to orientation and predation, color vision is extremely important in mantis shrimp behavioral displays (Cronin et al. 2006). As evidence, many of the coral-dwelling gonodactylids show bright, contrasting, species-specific color markings on raptorial appendages, walking legs, antennal scales, antennules, maxillipeds, pleopods, and uropods. Often the long setae framing the antennal scales, pleopods, and uropods are a different bright color than the supporting appendage (Reaka and Manning 1981). In addition to bright

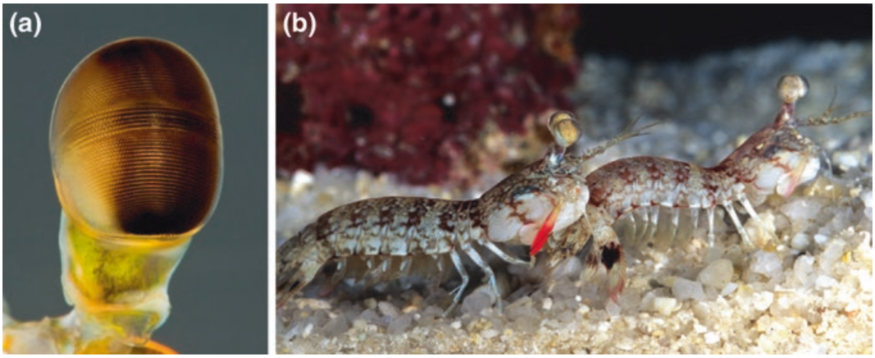


Fig. 2.3 Vision. **a** Eye of a *Hemisquilla californiensis* juvenile male. **b** Male and female *Odontodactylus latirostris*. The photo was taken with a polarizing filter showing that the male antennal scales are polarized, the female scales are not

colors on appendages, some smashers reveal contrasting meral spots on the raptorial appendages (Reaka and Manning 1981). Contrasting colors on appendages are important in transmitting agonistic intent, and may signal species and sex (Cheroske and Cronin 2005).

Some stomatopods have patches on their antennal scales, maxillipeds or uropod scales that structurally polarize light (Cronin et al. 2003). Stomatopods appear to recognize polarized-light features of a visual stimulus (Marshall et al. 1999) suggesting that mantis shrimps use light polarization analogously to color. Among the taxa that have the ability to polarize light, potential polarized light signals appear to become more common with increased habitat depth (Cronin et al. 2003). These signals, in addition to augmenting color patterns, may provide a private line of communication. The use of polarized signals is more prevalent among the smashers than among the spearers. A few species, such as *Haptosquilla trispinosa*, show dimorphic polarization, promoting sex recognition (Chiou et al. 2011). These signals are usually on the antennal scales and uropods (Fig. 2.3).

Smashers tend to be diurnal and to live in clear water, while spearers are more commonly nocturnal, or live in turbid environments with soft substrates. While coral-dwelling smashers have the acute vision described above, spearer eyes are better adapted for the detection of prey at short distances in dim light.

Individual Recognition Using Visual Cues

Individual recognition can rely on visual cues. Experiments were performed in which a focal *Haptosquilla glyptocercus* was allowed to observe one of two other conspecifics matched by sex and size but with different coloration (Cronin et al. 2006). This initial observation lasted an hour. The animal was then allowed to view either the originally observed conspecific again, or the other, novel size and sex matched but differently colored, conspecific. These tests showed that 83 % were more attentive to novel animals, measured as percent time poised with eyestalks beyond the entrance of its burrow. Since the focal animal was isolated from all but visual cues, this suggests the important of visual cues in differentiating animals. This type of visual identification of individuals would be expected to occur in species, like *H. glyptocercus*, that exist in many color morphs and occur in high densities with many burrows in close proximity in open habitat. *P. ciliata* would be another candidate.

Another piece of evidence suggesting the importance of visual cues is the role of bluffing. Bluffing is when stomatopods engage in an aggressive display without being willing and/or able to fight. For example, molting or newly molted *N. bredini* will continue to produce intense meral spread threat displays during cavity defense, even though their soft exoskeleton makes striking impossible. *N. bredini* bluff when facing smaller intruders, who are likely to be deterred by the (false) threat (Adams and Caldwell 1990). The newly molted residents tend to flee when the intruder is larger than they are, or if the bluffing leads to escalation rather than deterrence. The strategy appears to work: residents that do bluff were more likely to retain their cavities and less likely to sustain injury than animals that neither fled nor threatened (Adams and Caldwell 1990). Mantis shrimp appear to pave the way for future bluffing success by performing extra meral spread threat displays in the days leading up to their molt (Caldwell 1986b). This strategy only works if animals learn to recognize their neighbors, and are attentive to visual (as well as to chemical) displays.

The Social Roles of Auditory Cues

Auditory Sensory System

No true pressure-sensitive ear-like structures have been found in any crustaceans yet studied, and crustaceans have no air-filled cavities. As a result, crustaceans are not thought to be able to detect far-field, or pressure, component of sound (Breithaupt and Tautz 1990; Popper et al. 2001). Therefore, any response to sound has to be to the near-field, or particle displacement, component of sound (Breithaupt and Tautz 1990). Stomatopods do not appear to have any specialized structures, but they do have distributed surface setae and internal proprioceptors that are likely to respond to vibrational displacements in the water (Staaterman et al. 2011). In mantis shrimp, these mechanoreceptors are mostly simple, smooth, tapered setae varying from 50 to 2000 μm long (Schram et al. 2013). Experiments in copepods indicate that the smaller setae are more sensitive to higher frequency signals while the longer setae respond more to low frequency stimuli (Fields et al. 2002). Mantis shrimp setae appear to be in an appropriate size range for the detection of environmentally and socially relevant acoustic and hydrodynamic signals (Schram et al. 2013).

Auditory Cues and Behavior

Two sounds known to be made my mantis shrimp include the rumble made by *H. californiensis*, and the click made when stomatopods strike their raptorial appendages against another animal's carapace or against a hard surface.

H. californiensis males (and possibly females) produce a low-frequency rumble by vibrating their posterior mandibular remoter muscles (Patek and Caldwell 2006). The vibration may mark territory or attract females (Staaterman et al. 2011). These sounds may contain information about size and sex (Caldwell, *pers. obs.*). These rumbles have a dominant frequency of 167 Hz, with a range of 53–257 Hz (Staaterman et al. 2011). The near-field vibrational component of sound travels five times farther in sea water than in air. Therefore, the *Hemisquilla* rumble is probably perceptible at least nine meters from the source, making it likely that other mantis shrimp living in nearby burrows can detect these stimuli (Staaterman et al. 2011). *Lysiosquillina* make a similar rumble, but it has not been investigated. There is no evidence that rumbles are used in individual recognition.

Clicks can occur at various points during aggressive contests over shelters. A resident may strike the lip or wall of the cavity, producing a loud warning click. Or, a resident may strike the intruder, or vice versa. Sometimes, the winner of a contest will strike the substrate in a "victory display," reinforcing the win (Caldwell 1987). Researchers collecting data can hear the click, even if it occurs within the burrow. Both smashers and spearers use clicks. There is no evidence that clicks are used in individual recognition, but it is possible that clicks convey information about animal size in addition to serving as a general warning (Taylor and Patek 2010). Although not explicitly tested, it seems likely that molt stage might affect some of the properties of the strike signal as well.

Multimodal Signals Enhance Communication

The fierce competition for burrow space experienced by many mantis shrimp, combined with the potentially lethal weapons at their disposal, places a premium on rapid, accurate information that can reduce the risk involved in assessing and fighting other stomatopods and other dangerous competitors. Multimodal communication may enhance the information content or signal accuracy (Hebets and Rundus 2011).

One example of the importance of two sensory modalities is in the intersection of stomatopod visual and olfactory systems. Visual signaling plays a large role in gonodactylids, which are active in the daytime, are brightly colored, live in clear water in fairly high light areas, and have excellent vision. Even so, their sense of smell is likely to provide cues that may contain more (and possibly more reliable) information than visual cues (Christy and Rittshof 2011). Furthermore, for an animal anxious to probe the unseen occupant of a cavity, odor provides a channel of reliable information without requiring potentially dangerous intimate contact.

This is important because the hidden cavity resident can easily see intruders in the open and can at least assess the size and vigor of their opponent, and because possession of a shelter poses a distinct positional advantage. Thus, olfactory information can help to assuage the often asymmetrical transfer of information inherent in the visual system of cavity-dwellers.

The integration of sensory systems may be especially critical when environmental conditions favor one modality over another. For example, visual information can be compromised by low light levels (at night or in turbid environments), extraneous light in the environment, or the animal's position in its cavity or burrow. Recent work indicates that stomatopods increase their antennular flicking under low light conditions, presumably relying more on olfactory cues and less on visual cues under these circumstances (Cheroske et al. 2009).

In a potentially synergistic interweaving of vision and sound, *H. californiensis* may be able to see a visual analog of the carapace vibration created during rumbling. As described above, *H. californiensis* produce a low-frequency rumble by vibrating their posterior mandibular remoter muscles (Patek and Caldwell 2006). The males also have linearly polarized red patches along the sides of their carapace, merus, and proximal portions of their antennules. The muscles thought to drive the acoustic signaling are very near the carapace color patches. The flexing and relaxing of the carapace at 20–60 Hz could lead to a rapidly alternating pattern of polarization. Gonodactylids, including *H. californiensis,* are capable of detecting polarization (Cronin et al. 2000). If the flicker fusion frequency of ommatidia of *H. californiensis* is faster than 20–60 Hz, then *H. californiensis* should be able to detect changes in the patch polarization, reinforcing and possibly extending the acoustic signal. If individual males vibrate at characteristic frequencies, this could serve to assist individual recognition.

As indicated by the "victory display" strike of *N. bredini*'s raptorial appendage on the substrate after evicting an opponent, sound cues can reinforce the chemical signals also being sent. Obviously, there are many ways that signals can be combined to increase signal fidelity and avoid potentially lethal combat, and this is likely to be a fruitful area for future research.

Summary

Individual recognition occurs in only a subset of stomatopods, but for them, it plays several important roles. Often, these roles revolve around control of shelters. Contests over shelters can be critical for survival, as defensible cavities of the appropriate size are limited, are almost always already occupied, and predation risks outside shelters are high. By identifying and remembering specific individuals, and adjusting their behavior in consequence, mantis shrimp can more accurately decide whether or not to engage in a particular aggressive contest over a shelter. Through rapid identification of specific cavity residents who lost in previous contests, would-be intruders can choose their battles and increase their chances of success while minimizing injury. By recognizing their pair-bonded mate, *Lysiosquillina* avoid fighting every time they return to their shared burrow. In general, avoiding aggressive contests with previous mates (at least during the current breeding cycle) keeps would-be intruders from destroying their genetic legacy. Alternatively, avoiding previous mates altogether and constantly seeking new ones is another approach to reproductive success!

The pressure to develop individual recognition, and the resultant ability, varies among stomatopod groups. Species facing the greatest competition for cavities, the greatest replacement cost, and/or the most vulnerability outside the shelter are most likely to improve their lot via individual recognition. The amount of repeated contact with a limited number of individuals over a period of time is also a factor. The capacity for individual recognition relies on the ability to differentiate individuals via multiple sensory cues, learning and memory, and behavioral flexibility. As these capabilities vary among stomatopod groups, so does the ability to recognize individuals.

References

Adams ES, Caldwell RL (1990) Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. Anim Behav 39:706–716

Aggio J, Derby CD (2011) Chemical communication in lobsters. In: Breihaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, New York, pp 239–256

Bok MJ, Porter ML, Place AR, Cronin TW (2014) Biological sunscreens tune polychromatic ultraviolet vision in mantis shrimp. Curr Biol 24:1–7

Breithaupt T (2001) Fan organs of crayfish enhance chemical information flow. Biol Bull 200:150–154

Breithaupt T, Tautz J (1990) The sensitivity of crayfish mechanoreceptors to hydrodynamic and acoustic stimuli. In: Wiese K, Krenz WD, Tautz J, Reichart H, Mulloney B (eds) Frontiers of crustacean neurobiology. Birkhäuser, Basel, pp 114–120

Caldwell RL (1979) Cavity occupation and defensive behaviour in the mantis shrimp Gonodactylus festae: evidence for chemically mediated individual recognition. Anim Behav 27:194–201

Caldwell RL (1982) Interspecific chemically mediated recognition in two competing stomatopods. Mar Behav Physiol 8:189–197

Caldwell RL (1985) A test of individual recognition in the mantis shrimp *Gonodactylus festae*. Anim Behav 33:101–106

Caldwell RL (1986a) Withholding information on sexual condition as a competitive mechanism. In: Drickamer LC (ed) Behavioral ecology and population biology. Privat, Toulouse, pp 83–88

Caldwell RL (1986b) The deceptive use of reputation by stomatopods. In: Mitchell RW, Thompson NS (eds) Deception: perspectives on human and non-human deceit. State University of New York Press, New York, pp 129–145

Caldwell RL (1987) Assessment strategies in stomatopods. Bull Mar Sci 41:135–150

Caldwell RL (1991) Variation in reproductive behavior in stomatopod crustacean. In: Bauer RT, Martin JW (eds) Crustacean sexual biology. Columbia University Press, New York, pp 67–90

Caldwell RL (1992) Recognition, signaling, and reduced aggression between former mates in a stomatopod. Anim Behav 44:11–19

Caldwell RL, Dingle H (1975) Ecology and evolution of agonistic behavior in stomatopods. Naturwissenschaften 62:214–222

Caldwell RL, Dingle H (1976) Stomatopods. Sci Am 234:80–89

Caldwell RL, Lamp K (1981) Chemically mediated recognition by the stomatopod *Gonodactylus bredini* of its competitor, the octopus *Octopus joubini*. Mar Behav Physiol 8:35–41

Cheroske AG, Cronin TW (2005) Variation in stomatopod (*Gonodactylus smithii)* color signal design associated with organismal condition and depth. Brain Behav Evol 66:99–113

Cheroske AG, Cronin TW, Durham MF, Caldwell RL (2009) Adaptive signaling behavior in stomatopods under varying light conditions. Mar Freshw Behav Physiol 42:219–232

Chiou TH, Marshall NJ, Caldwell RL, Caldwell TW (2011) Changes in light-reflecting properties of signaling appendages alter mate choice behavior in a stomatopod crustacean *Haptosquilla trispinosa*. Mar Freshw Bevah Physiol 44:1–11

Christy JH, Rittschof D (2011) Deception in visual and chemical communication in crustaceans. In: Breihaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, New York, pp 313–334

Christy JH, Salmon M (1991) Comparative studies of reproductive behavior in mantis shrimps and fiddler crabs. Am Zool 31:329–337

Cronin TW, Caldwell RL, Marshall J (2006) Learning in stomatopod crustaceans. Int J Comp Psychol 19:297–317

Cronin TW, Marshall NJ, Caldwell RL (2000) Spectral tuning and the visual ecology of mantis shrimps. Philos Trans Roy Soc B 355:1263–1267

Cronin TW, Shashar N, Caldwell RL, Marshall J, Cheroske AG, Chiou T-H (2003) Polarization vision and its role in biological signaling. Integr Comp Biol 43:549–558

Derby CD, Fortier JK, Harrison PJH, Cate HS (2003) The peripheral and central antennular pathway of the Caribbean stomatopod crustacean *Neogonodactylus oerstedii.* Arthropod Struct Dev 32:175–188

Fields DM, Shaeffer DS, Weissburg MJ (2002) Mechanical and neural responses from the mechanosensory hairs on the antennule of *Gaussia princeps.* Mar Ecol Prog Ser 227: 173–186

Hallberg E, Johansson KUI, Elofsson R (1992) The aesthetasc concept: structural variations of putative olfactory receptor cell complexes in Crustacea. Microsc Res Tech 22:325–335

Hatziolos ME, Caldwell RL (1983) Role reversal in the stomatopod *Pseudosquilla ciliata* (Crustacea). Anim Behav 31:1077–1087

Hebets EA, Rundus A (2011) Chemical communication in a multimodal context. In: Breihaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, New York, pp 335–354

Marshall NJ (1988) A unique colour and polarization vision system in mantis shrimps. Nature 333:557–560

Marshall NJ, Land MF (1993) Some optical features of the eyes of stomatopods. I. Eye shape, optical axes, and resolution. J Comp Physiol A 173:565–582

Marshall NJ, Cronin TW, Shashar N (1999) Behavioral evidence for polarization vision in stomatopods reveals a potential channel for communication. Curr Biol 9:755–758

Marshall J, Cronin TW, Kleinlogel S (2007) Stomatopod eye structure and function: A review. Arthropod Struct Dev 36:420–448

Mead KS, Caldwell RL (2011) Mantis shrimp: olfactory apparatus and chemosensory behavior. In: Breihaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, New York, pp 219–238

Mead KS, Minshall H (2012) Burrow and current production by the mantis shrimp, *Squilla empusa*. Am Acad Underwater Sci Sci Symp Proc 31:181–185

Mead KS, Weatherby TM (2002) Morphology of mantis shrimp chemosensory sensilla facilitates fluid sampling. Invertebr Biol 121:148–157

Mead K, Koehl MAR, O'Donnell MJ (1999) Mantis shrimp sniffing: the scaling of chemosensory sensilla and flicking behavior with body size. J Exp Mar Biol Ecol 241:235–261

Mead K, Koehl MAR (2000) Particle image velocimetry measurements of fluid flow through a model array of mantis shrimp chemosensory sensilla. J Exp Biol 203:3795–3808

Montgomery EL, Caldwell RL (1984) Aggressive brood defense by females in the stomatopod *Gonodactylus bredini*. Behav Ecol Sociobiol 14:247–251

Patek SN, Caldwell RL (2006) The stomatopod rumble: low frequency sound production in Hemisquilla californiensis. Mar Freshw Behav Physiol 39:99–111

Popper AN, Salmon M, Horch KW (2001) Acoustic detection and communication by decapod crustaceans. J Comp Phys A 187:83–89

Reaka RL, Manning RB (1980) The distributional ecology and zoogeographical relationships of shallow water stomatopod Crustacea from Pacific Costa Rica. Smithson Contrib Mar Sci 7:1–29

Reaka ML, Manning RB (1981) The behavior of stomatopod Crustacea and its relationship to rates of evolution. J Crust Biol 1:309–327

Schmidt M, Mellon D (2011) Neuronal processing of chemical information in crustaceans. In: Breihaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, New York, pp 123–148

Schram FR, Ahyong ST, Patek SN, Green PA, Rosario MV, Bok MJ, Cronin TW, Vetter KSM, Caldwell RL, Scholtz G, Feller KD, Abello P (2013) Subclass hoplocarida calman 1904, order Stomatopoda Latreille, 1817. In: von Vaupel Klein JC, Charmantier-Daures M, Schram FR (eds) Treatise on zoology-anatomy, taxonomy, biology, vol 4A, The Crustacea. Brill Academic Publishers, Netherlands, pp 179–356

Shuster SM, Caldwell RL (1989) Male defense of the breeding cavity and factors affecting the persistence of breeding pairs in the Stomatopod *Gonodactylus bredini* (Manning) (Crustacea: Hoplocarida). Ethology 82:192–207

Staaterman ER, Clark CW, Gallagher AJ, deVries MS, Claverie T, Patek SN (2011) Rumbling in the benthos: acoustic ecology of the California mantis shrimp *Hemisquilla californiensis*. Aquat Biol 13:97–105

Taylor JRA, Patek SN (2010) Ritualized fighting and biological armor: the impact mechanics of the mantis shrimp's telson. J Exp Biol 213:3496–3504

Thoen HH, How MJ, Chiou T-H, Marshall J (2014) A different form of color vision in mantis shrimp. Science 343:411–413

Wickler W (1973) Biology of hymenocera picta dana. Micronesica 9:225–230

Wickler W, Seibt U (1981) Monogamy in crustacean and man. Z Tierpsychol 57:215–234

Chapter 3
To What Extent Can Freshwater Crayfish Recognise Other Crayfish?

Blair W. Patullo and David L. Macmillan

The ability for sophisticated and flexible recognition by vertebrates has been known for a very long time, probably because it features so strongly in human social behaviour and is therefore easily recognised in other species. As evidenced by the increasing number of studies and reports (Tibbets and Dale 2007), recent years have seen increased interest in the occurrence and properties of this response in non-vertebrates where it may not be so easily identified. Studies have now been undertaken on a wide range of organisms exemplified by the chapters of this review collection but our understanding of this phenomenon is still at an early stage and we can make few generalisations beyond its wide occurrence. In retrospect, its incidence should not be surprising. The advantages that it confers are apparent so that, all things being equal, it should be selected for. What characteristics of life history and interaction with con-specifics are likely to predict its presence and what factors predict the level of sophistication and flexibility? These questions remain to be answered but, based on what has already been discovered, we postulate here that it will evolve wherever there is a capacity for analysis of sensory signals that carry identifying information.

The focus of our chapter is to summarise the present state of knowledge concerning recognition in freshwater crayfish. When discussing this topic, it is not possible to consider crayfish alone because, at this stage, only limited data are available from crayfish species. So here we will refer to some findings from lobsters and other decapod species to provide a context for linking the known elements for crayfish. In the text we use the various degrees of "recognition" according to the definitions developed by Gherardi et al. (2005). We will deal with chemical recognition first, then with visual recognition and, even though there is a

---

B.W. Patullo · D.L. Macmillan (✉)
The Department of Zoology, The University of Melbourne,
Parkville, VIC, 3010, Australia
e-mail: d.macmillan@unimelb.edu.au

B.W. Patullo
e-mail: blairpatullo@gmail.com

L. Aquiloni and E. Tricarico (eds.), *Social Recognition in Invertebrates*,
DOI 10.1007/978-3-319-17599-7_3

dearth of information, the intriguing matter of the relationship between the two—multimodal recognition. Along the way we will briefly mention some of the similarities to and differences from other invertebrates (reviewed more fully elsewhere e.g. Tibbetts and Dale 2007; Breithaupt and Thiel 2011) and will finish with some speculation about the evolution of recognition in crayfish and strategies for testing such hypotheses.

Social Behaviour and Hierarchies—A Valuable Paradigm for Crayfish Recognition Research

Investigations of recognition between crayfish conspecifics has predominantly involved dominance pairs or hierarchies established during competition for mates, shelter and food. It is by experimental manipulation of these encounters that the mechanisms and quality of recognition can be elucidated. The literature on staged encounters is extensive and has spanned more than half a century so we only consider here the key elements for recognition in the present context. It has been used, for example, to investigate the separation of class recognition (e.g. gender and dominance) from individual recognition (Gherardi et al. 2005).

Like many decapods, social crayfish establish dominance hierarchies of some complexity (e.g. Bovbjerg 1953, 1956; Daws et al. 2011) but the durability of these are not as well understood as those in lobsters, although there is some evidence that they are not as long-lasting (Bergman et al. 2003). The hierarchies are established on the basis of success in physical encounters—contest encounters—apparently made up of relatively common, stereotyped sequences across species (Moore 2007). These typically involve meral-expansion threat displays which, if they do not deter the contest partner, may be followed by claw grasping, wrestling and claw ripping leading to damage to the body and limbs. Eventually one contestant, the loser, retreats. None of this requires recognition by the contestants. The evidence for recognition comes from the interaction between individuals when they meet subsequently (e.g. Fig. 3.1). It would, in principle, be possible for contestants to test their standing against other crayfish by engaging in a series of short fights. As in most animal social systems, however, the value of avoiding potentially damaging physical encounters by both winners and losers is such that mechanisms evolve to render a rematch unnecessary or of reduced intensity to avoid physical harm to the protagonists.

Research with staged encounters has provided the foundation for the majority of recognition studies because it relates critical factors to controls for testing when recognition is occurring. Winner-loser effects, for example, aggression, isolation and hierarchy formation are known to alter crayfish behaviour and need to be considered in good experimental design (e.g. Bovbjerg 1953; Issa et al. 1999; Goessmann et al. 2000; Daws et al. 2002; Bergman et al. 2003; Baird et al. 2006; Hemsworth et al. 2007; Patullo et al. 2009). Most of our discussion here comes from research that considered these factors.

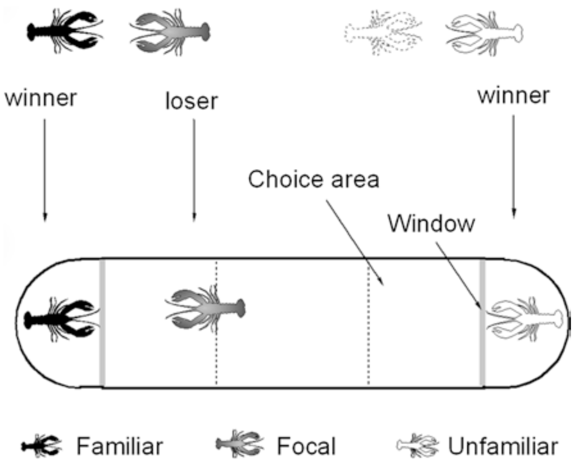


Fig. 3.1 Social encounters can be combined in test paradigms to demonstrate recognition. In this example, pairs of crayfish (*top*) meet and establish social rank or winning ability. A focal animal is placed in a test arena (*bottom*), in this case the losing crayfish from one of the previous encounters. Recognition is then tested by offering a choice between crayfish at either ends of the arena, which are visible to the focal crayfish through transparent windows. Status is controlled in the process by careful selection of the right combinations of crayfish in the ends, between winners and losers and familiar versus unfamiliar animals from the first encounter. Further detail Van der Velden et al. (2008)

Chemical Communication and Recognition in Crayfish

Like all aquatic crustaceans, crayfish possess many chemoreceptors (Bullock and Horridge 1965; Atwood and Sandeman 1982; Breithaupt and Thiel 2011). These may be found on all areas of the body but are concentrated on the antennules, antennae, mouthparts and at the tips of the pereiopods. Numerous studies indicate that they are used in social communication and are responsible, although not necessarily exclusively, for recognition (e.g. Breithaupt 2011, research summarised in Hemsworth et al. 2007 and more widely in other crustaceans Breithaupt and Thiel 2011).

The most effective systems permit recognition to occur at a distance without need for physical contact. The main source of chemical information available between conspecifics is broadcast in urine expelled from a small, anterior nephropore opening near the base of the antennae. Lobsters and other decapods can control the timing and direction of the urine stream (Aggio and Derby 2011) and there is increasing evidence that crayfish do the same, from incidental behavioural observations and the anatomical structures to facilitate it (Breithaupt and Eger 2002; Berry and Breithaupt 2010 and others cited in Breithaupt 2011). Information on the nature of the substances within the urine that are responsible for the communication between decapods is fragmentary and almost non-existent for crayfish. Discovering how species- and function-specific these are is an important objective for future research.

In clawed lobsters, where the most extensive studies have taken place, the most important receivers of urine signals are the aesthetasc hairs on the antennules (Hallberg and Skog 2011), although similar receptors are found elsewhere, particularly on the mouthparts and periopods (Johnson et al. 1984). Interference by amputation or mechanical blocking of the hairs to reduce or remove the signals appear to reduce or even abolish transfer of sexual information (*Homarus americanus*, Bushman and Atema 1997) although there may be some gender differences in the other homarid species (*H. gammarus*—Skog 2009a, b). Dominance information is also eliminated by similar experiments (Karavanich and Atema 1998a, b; Johnson and Atema 2005).

Those social crayfish studied thus far most commonly establish dominance hierarchies, but there is evidence of differences in the way the information for them is received and the way they are established and maintained. The situation in crayfish is similar to that found in lobsters in some aspects. *Procambarus clarkii* formed enduring hierarchical structures which ensure that fights with former winning opponents were either avoided or were shorter in duration than those between previously known animals (Horner et al. 2008). Shorter duration of subsequent encounters also occurred in *Astacus leptodactylus* (Breithaupt and Eger 2002). Furthermore, interference with the aesthetascs after an initial encounter resulted in behaviour more similar in duration and intensity to initial encounters than if the aesthetascs were not manipulated. A similar outcome was observed in fights between *Orconectes rusticus* with the important exception that the memory of opponents appeared to last for only about 60 min (Bergman et al. 2003). Recognition in this species is probably less sensitive or situation-specific than in *P. clarkii* because "winner" odour in the surrounding water influenced the outcome of encounters even if it was not from a former opponent and the outcome of choices in Y-mazes (Zulandt Schneider et al. 1999, 2001; Bergman and Moore 2005). This type of "status" recognition mechanism appears to be even more evident in *A. leptodactylus* and *Procambarus acutus* which show clear "former winner" and "former loser" behaviour whether or not they have previously encountered the opponent (Breithaupt and Eger 2002; Gherardi and Daniels 2003).

Examples mentioned throughout the reviews in this collection and in that of Breithaupt and Thiel (2011) reveal many more details of a rich diversity in signalling mechanisms and outcomes. We have barely scratched the surface of this variation in crayfish but, given the range of ecological situations in which crayfish live, diversity rather than conformity must be expected. Following a study of communication in *A. pallipes* which did not appear to match the then known commonalities of sexual communication in crayfish, Acquistapace and colleagues proposed that the diverse natural history of crayfish species would be found to mediate multiple variations in communication systems (Acquistapace et al. 2002).

Individual recognition is more difficult, and quite laborious to establish experimentally than class or group recognition. To date, the only convincing method for establishing the presence of individual recognition is to test for evidence following staged encounters using devices such as choice experiments or a second round of fighting. Examples of assessment in choice experiments include those in which losers of contests are given options between the winner of one of their earlier contests and a matched (size, colour, gender etc.) unfamiliar winner of a contest in which the focal loser was not involved. The focal animal then demonstrates that it can recognise the familiar animal by a non-random preference for the winner or loser (e.g. Crook et al. 2004, Fig. 3.1). Paradigms to test individual recognition by successive fights were applied to chemical recognition of urine in the lobsters before crayfish (Karavanich and Atema 1998a, b). A number of studies suggest that the ability for individual chemical recognition is also present in some crayfish species but it has not yet been definitively demonstrated. There is evidence that *C. destructor*, which can use visual information for individual recognition of previous opponents (see below and Fig. 3.1), can also use chemical information for this purpose but the design of the experiment did not entirely preclude familiar recognition (Crook et al. 2004). Similarly, conclusions from outcomes of second rounds of fights between *C. dispar* (Seebacher and Wilson 2007) and those following observation of contests in *P. clarkii* (Aquiloni et al. 2012) suggest that individual recognition could exist, although the experiments do not preclude the possibility of explaining the result by status recognition or experience. Given the intensity of research across several genera of crayfish we predict that this will be confirmed experimentally for additional species shortly.

Visual Communication and Recognition in Crayfish

Studies of crustacean eyesight reveal that stomatopods have the most advanced vision in the Class Crustacea (e.g. Marshall et al. 1996; Chiao et al. 2000; Cronin et al. 2001). Crayfish vision is not thought to be as advanced, but vision is important in many behavioural situations. Crayfish change behaviour in response to visual cues of various shape, size and colour (wavelength) indicating that sight is a valuable sense in their world.

Crayfish have at least one photosensitive pigment and receptor system (Kennedy and Bruno 1961). There is also conflicting evidence that supports the presence of a second pigment and receptor system (Wald 1967). In agreement, is that crayfish can detect different wavelengths of light throughout most of the colour spectrum that is visible to humans. The peak sensitivity of the main system is at about 570 nm, yellow, and this decreases as wavelengths approach 650 nm, red (Kennedy and Bruno 1961).

What does this visual ability mean to a crayfish? At the simplest level, objects and shadows will cause behavioural change. Waving a human hand over the body can cause the animal to react and adopt a posture known as the defence response where the abdomen extends, the animal arches its back and spreads its chelae (Kelly and Chapple 1990). Other threatening shadows and looming objects also induce defensive reactions in *P. clarkii* (Glantz 1974a, b, 1978; Beall et al. 1990). Further to this, fights between individuals of the crayfish *O. rusticus* last longer and occur at a more intense level in dim light compared with the same behaviour

Fig. 3.2 Greebling on a crayfish. Different coloured patches added to a crayfish body are used to determine focus areas of visual recognition in *Cherax destructor*. Further detail in Van der Velden et al. (2008)

observed in bright light (Bruski and Dunham 1987). Female *P. clarkii* also need visual cues before they can distinguish a male mate (Aquiloni et al. 2009). The last two examples indicate that crayfish pay attention to visual cues beyond shadows so that recognising another crayfish may reveal the importance of this sense.

From shadows to shapes, greebles were the main method used to demonstrate that this visual acuity was sophisticated enough to recognise body parts and thus vision could be a modality used to recognise another individual. The art of greebling involved modifying the appearance of an animal with controlled artificial forms to test hypotheses (Gauthier and Tarr 1997, Fig. 3.2). So just as a human could distinguish two similar people by looking at hats on their heads, for example a magician's cylindrical top hat from a Mexican's conical wide-brimmed sombrero, research showed crabs could distinguish one another based on objects attached to their backs (Hazlett 1972). The addition of other greebles, such as artificial markings, has demonstrated similar results in a range of invertebrates (Dunham 1978; Vannini and Gherardi 1981; Detto et al. 2006). This raises the question of whether or not crayfish can also analyse body features of an individual to recognise it later and, if so, what parts of the body are important to remember. Evidence in two species suggests crayfish can do this.

Cherax destructor prefers to spend more time closer to an individual it has met during a previous fight rather than with an unfamiliar crayfish when only visual cues of the opponent are available to make judgment (Crook et al. 2004). This confirms that *C. destructor* is capable of binary recognition between the familiar and the unfamiliar. This response is consistent with dear enemy theory where animals prefer to spend time with familiar individuals, even if they are stronger, rather than battle with the unknown and risk higher energetic cost (Fisher 1954).

In addition, *P. clarkii* is attracted to it's reflection in mirrors (Drozdz et al. 2006; May and Mercier 2006). This discovery could be evidence of a form of visual self-recognition similar to that of humans recognising their own reflection. It needs further testing, however, because the outcome was different depending on the social status of the crayfish (May and Mercier 2006). That is, *P. clarkii* may only recognise its reflection as a "crayfish", not as itself, or only be responding to movement of an object.

The familiar recognition and potential self-recognition experiments with *C. destructor* and *P. clarkii* demonstrate that a focal crayfish can recognise up to two individuals. Aquiloni and Gherardi (2010), Aquiloni et al. (2010) suggest the

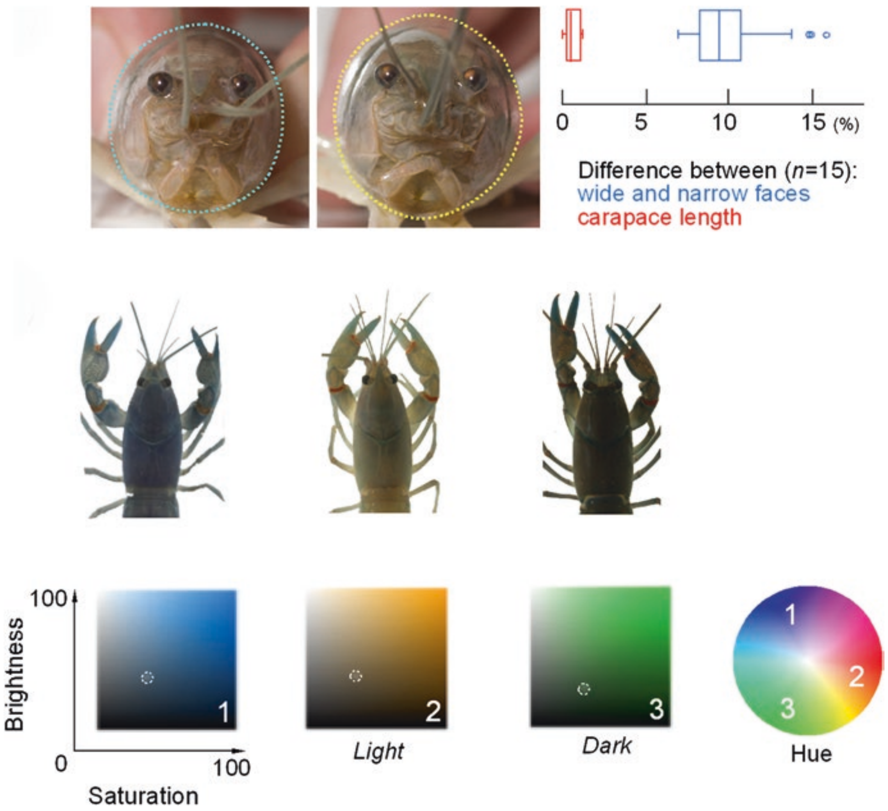


Fig. 3.3 Variation in visual features of *Cherax destructor*: facial width (*top*) and colour (*middle and bottom*). Further detail in Van der Velden et al. (2008)

ability is more advanced because they demonstrated that *P. clarkii* can distinguish between three crayfish. They allowed a female to watch two males fight and then gave the female a visual choice between one of those males and a third, unfamiliar male. The female spent more time in the vicinity of the familiar male. This outcome suggests that true individual recognition is present in some crayfish and provides another possible reason why crayfish might recognise one another—in sexual selection to identify optimal mates.

A combination of visual clues must be analysed for successful recognition of multiple individuals. Markings on the anterior carapace, natural colour of the carapace and facial width are three features that *C. destructor* can recognise (Van der Velden et al. 2008, Figs. 3.2 and 3.3). It is not possible to determine the exact physical features being analysed in the Van der Velden et al. (2008) study because facial width may, for example, be correlated to other physical attributes such as body size. Nonetheless, colour and facial width were not correlated so this species must be using at least a small matrix of cues to remember each animal it meets (Fig. 3.3).

The extent of the matrix of important visual clues to identity and the number of unique individuals able to be remembered may be increase by future investigation. To date however, crayfish recognition research has been limited to paradigms where opponents fight, whether it is to monitor behavior in that fight or a fight prior to an experimental test. This approach may not easily lend itself to testing interactions beyond those currently known and may require a new strategy to reveal the full complexity of crayfish visual recognition.

Multimodal Communication and Recognition in Crayfish

Crayfish are likely to benefit if they can use more than one sense to communicate because in the wild conditions vary. Water can range from being stagnant to high flowing and turbidity can fluctuate (Merrick 1991). A changing local environment means that not all modes of communication will be available all the time so survival should favour species with multiple information channels that permit them to apply the best sense for the presenting conditions. We are probably yet to know how flexible crayfish are in this respect, but the number of reports of evidence for multimodal communication in crayfish is on the increase. Callaghan et al. (2012) showed that chemical, tactile and visual information can be used by *O. rusticus* in the establishment of hierarchies. By interfering with each of these modalities in turn they showed that in this species under the test circumstances the effectiveness ranking is chemical > tactile > visual. Bouwma and Hazlett (2001) also investigated multiple modalities, but only investigated two sensory pathways. They revealed that both visual and chemical cues are used by *Orconectes propinquus* to detect fish predators.

There is also increasing evidence that one crayfish can use multiple senses to recognise another. Both visual and chemical information can be used in gender recognition between individuals of the species *A. pallipes* (Acquistapace et al. 2002). Gender recognition may also influence subsequent encounters in *P. clarkii,* along with mate choice and eavesdropping—one crayfish observing fights between others (Aquiloni and Gherardi 2008; Aquiloni et al. 2009). Both visual and chemical information are also important in communication between familiar *C. destructor* opponents as mentioned in previous sections here (Crook et al. 2004).

Crayfish have a very keen tactile sense with which to explore their environment (Sandeman and Varju 1988; Basil and Sandeman 2000; McMahon et al. 2005; Patullo and Macmillan 2006) and it is likely that this also plays a part in agonistic behaviour, particularly in nocturnal species or those living in turbid waters. There is, for example, some evidence that *C. destructor* combines chemical information and tensile force monitored by its claws in the establishment of dominance relationships (Seebacher and Wilson 2007). So it is likely that we have not yet revealed the full skill set of how crayfish use multiple senses, not only for recognition but also in other parts of their everyday lives.

Sorting out the use and extent of multimodal systems is challenging but the issues involved speak to some very interesting questions in behaviour and its evolution. For example, to what extent are their residual abilities for the availability of a parallel information channel if it is not used for a significant evolutionary period? What neural changes are likely to accompany this situation? What would this tell us about the cost of maintaining a disused channel? The variability of crayfish biology adds to the intrigue of how and why animals evolve their senses. Thus, they form a particularly attractive group for gaining insight into these kinds of behavioural evolutionary questions, adding to the other advantages already advocated by others (see reviews in Breithaupt and Thiel 2011).

Making Sense of Diversity

It is clear that the information on recognition in social crayfish is fragmentary and related only to a few popular study species so it is still too early to assemble the elements of the jigsaw into a coherent picture without extrapolation that includes evidence from other crustacean groups (Table 3.1). While it is tempting to use results from other crustacean species, particularly other decapods to fill in the gap, it should be clear from our brief survey here that this is likely to be a productive enterprise only insofar as it informs us about the range of described possibilities and so assist us when embarking on research with new species.

It appears to us that we will gain a better understanding of not only recognition in crayfish, but also of the biological role of their communication, if we seek to study crayfish with particular ecological niches or needs and to compare the differences in communication systems employed. We advocate, for example, comparisons between crayfish living in lotic versus lentic environments, those with nocturnal habits against those with diurnal ones, those from clear waters versus those from turbid ones and so forth, the list is extensive. In this way we might hope to build a matrix of recognition responses based on biological factors. This understanding of the biological reasons for the evolution of particular

Table 3.1 A summary of the different levels of recognition across crayfish species demonstrated so far. Six species across four genera have been the main focus of research. They have revealed evidence for at least five potential types, or levels, of recognition. Compiled from references included in the text

Level of recognition	Species
True individual	*P. clarkii, C. destructor*
Familiar	*P. clarkii, C. destructor*
Gender (class)	*P. clarkii, A. pallipes*
Status/social rank (class)	*P. clarkii, P. acutus, A. leptodactylus, C. dispar, C. destructor*
Self(class)*	*P. clarkii*

* May vary depending on interpretation of methods and results.

communication strategies should permit us to predict the likelihood that a particular species will exhibit certain characteristics of recognition in its communication.

Acknowledgments We thank the two reviewers who helped to improve this manuscript and we gratefully acknowledge the contribution of the late Francesca Gherardi in the development of our understanding of so many aspects of crayfish behaviour.

References

Acquistapace P, Aquiloni L, Hazlett BA et al (2002) Multimodal communication in crayfish: ex recognition during mate search by male Austropotamobius pallipes. Can J Zool 80:2041–2045

Aggio J, Derby CD (2011) Chemical communication in lobsters. In: Breithaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, Berlin, pp 239–256

Aquiloni L, Gherardi F (2008) Assessing mate size in the red swamp crayfish Procambarus clarkii: effects of visual versus chemical stimuli. Fresh Biol 53:461–469

Aquiloni L, Gherardi F (2010) Crayfish females eavesdrop on fighting males and use smell and sight to recognize the identity of the winner. Anim Behav 79:265–269

Aquiloni L, Massolo A, Gherardi F (2009) Sex identification in female crayfish is bimodal. Naturewissenschaften 96:103–110

Aquiloni L, Buric M, Gherardi F (2010) Crayfish females eavesdrop on fighting males before choosing the dominant mate. Curr Biol 18:R462–R463

Aquiloni L, Goncalves V, Inghilesi AF et al (2012) Who's what? Prompt recognition of social status in crayfish. Behav Ecol Sociol 66:785–790

Atwood HL, Sandeman DC (eds) (1982) Neurobiology: structure and function. In: Bliss DE (ed) The biology of crustacea, vol 3. Academic Press, New York

Baird HP, Patullo BW, Macmillan DL (2006) Reducing aggression between freshwater crayfish (*Cherax destructor* Clark: Decapoda, Parastacidae) by increasing habitat complexity. Aqua Res 37:1419–1428

Basil J, Sandeman D (2000) Crayfish (*Cherax destructor*) use tactile cues to detect and learn topographical changes in their environment. Ethology 106:247–259

Beall SP, Langley DJ, Edwards DH (1990) Inhibition of escape tailflip in crayfish during backward walking and the defence posture. J Exp Biol 152:577–582

Bergman DA, Moore PA (2005) Prolonged exposure to social odours alters subsequent social interactions in crayfish (*Orconectes rusticus*). Anim Behav 70:311–318

Bergman DA, Kozlowski C, McIntyre JC et al (2003) Temporal dynamics and communication of winner-effects in the crayfish, *Orconectes rusticus*. Behaviour 140:805–825

Berry FC, Breithaupt T (2010) To signal or not to signal? Chemical communication by urine-borne signals mirrors sexual conflict in crayfish. BMC Biol 8:25

Bouwma P, Hazlett BA (2001) Integration of multiple predator cues by the crayfish *Orconectes propinquus*. Anim Behav 61:771–776

Bovbjerg RV (1953) Dominance order in the crayfish *Orconectes virilis* (Hagen). Physiol Zool 26:173–178

Bovbjerg RV (1956) Some factors affecting aggressive behaviour in crayfish. Physiol Zool 29:127–136

Breithaupt T (2011) Chemical communication in crayfish. In: Breithaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, New York, pp 257–276

Breithaupt T, Eger P (2002) Urine makes the difference: chemical communication in fighting crayfish made visible. J Exp Biol 205:1221–1231

Breithaupt T, Thiel M (eds) (2011) Chemical communication in crustaceans. Springer, Berlin

Bruski CA, Dunham DW (1987) The importance of vision in agonistic communication of the crayfish *Orconectes rusticus*: an analysis of bout dynamics. Behaviour 63:83–107

Bullock TH, Horridge GA (eds) (1965) Structure and function in the nervous systems of invertebrates. WH Freeman, San Francisco

Bushman PJ, Atema J (1997) Shelter sharing and chemical courtship signals in the lobster *Homarus americanus*. Can J Fish Aq Sci 54:647–654

Callaghan DT, Weisbord CD, Dew WA et al (2012) The role of various sensory inputs in establishing social hierarchies in crayfish. Behaviour 149:1443–1458

Chiao CC, Cronin TW, Marshall NJ (2000) Eye design and color signaling in a stomatopod crustacean *Gonodactylus smithii*. Brain Behav Evol 56:107–122

Cronin TW, Caldwell RL, Marshall J (2001) Sensory adaptation: tunable colour vision in a mantis shrimp. Nature 411:547–548

Crook R, Patullo BW, Macmillan DL (2004) Multimodal individual recognition in the crayfish *Cherax destructor*. Mar Fresh Behav Physiol 37:271–286

Daws AG, Grills J, Konzen K et al (2002) Previous experiences alter the outcome of aggressive interactions between males in the crayfish *Procambrus clarkii*. Mar Fresh Behav Physiol 35:139–148

Daws AG, Hock K, Huber R (2011) Spatial structure of hierarchical groups: testing for processes of aggregation, clustering, and spatial centrality in crayfish (*Orconectes rusticus*). Mar Fresh Behav Physiol 44:209–222

Detto T, Backwell PRY, Hemmi JM et al (2006) Visually mediated species and neighbour recognition in fiddler crabs (*Uca mjoebergi* and *Uca capricomis*). Proc R Soc B 273:1661–1666

Drozdz JK, Viscek J, Brudzynski SM et al (2006) Behavioural responses of crayfish to a reflective environment. J Crust Biol 26:463–473

Dunham DW (1978) Effect of chela white on agonistic success in a diogenid hermit crab (*Calcinus laevimanus*). Mar Behav Physiol 5:137–144

Fisher J (1954) Evolution and bird sociality. In: Huxley J, Hardy AC, Ford EB (eds) Evolution as a process. Allen & Unwin, London, pp 71–83

Gauthier I, Tarr MJ (1997) Becoming a "greeble" expert: exploring mechanisms for face recognition. Vision Res 37:1673–1682

Gherardi F, Daniels WH (2003) Dominance hierarchies and status recognition in the crayfish *Procambarus acutus acutus*. Can J Zool 81:1269–1281

Gherardi F, Tricarico E, Atema J (2005) Unraveling the nature of individual recognition by odor in hermit crabs. J Chem Ecol 31:2877–2896

Glantz RM (1974a) The visually evoked defense reflex of the crayfish: habituation, facilitation, and the influence of picrotoxin. J Neurobiol 5:263–280

Glantz RM (1974b) Defence reflex and motion detector responsiveness to approaching targets: the motion detector trigger to the defence reflex pathway. J Comp Physiol 95:297–314

Glantz RM (1978) Visual input and motor output of command interneurons of the defence reflex pathway in the crayfish. In: Hoyle G (ed) Identified neurons and behavior of arthropods. Plenum, New York, pp 259–274

Goessmann C, Hemelrijk C, Huber R (2000) The formation and maintenance of crayfish hierarchies: behavioral and self-structuring properties. Behav Ecol Sociobiol 48:418–428

Hallberg E, Skog M (2011) Chemosensory sensilla in crustaceans. In: Breithaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, Berlin, pp 103–122

Hazlett BA (1972) Stimulus characteristics of an agonistic display of the hermit crab (*Calcinus tibicen*). Anim Behav 20:101–107

Hemsworth R, Villareal W, Patullo BW et al (2007) Crustacean social behavioral changes in response to isolation. Biol Bull 213:187–195

Horner AJ, Schmidt M, Edwards DH et al (2008) Role of the olfactory pathway in agonistic behavior of crayfish, *Procambarus clarkii*. Invert Neurosci 8:11–18

Issa FA, Adamson DJ, Edwards DH (1999) Dominance hierarchy formation in juvenile crayfish Procambarus clarkii. J Exp Biol 202:3497–3506

Johnson ME, Atema J (2005) The olfactory pathway for individual recognition in the American lobster *Homarus americanus*. J Exp Biol 208:2865–2872

Johnson BR, Voigt R, Borroni PF et al (1984) Response properties of lobster chemoreceptors: tuning of primary taste neurons in walking legs. J Comp Physiol 155:5593–5604

Karavanich C, Atema J (1998a) Individual recognition and memory in lobster dominance. Anim Behav 56:1553–1560

Karavanich C, Atema J (1998b) Olfactory recognition of urine signals in dominance fights between male lobster, *Homarus americanus*. Behaviour 135:719–730

Kelly TM, Chapple WD (1990) Kinematic analysis of the defence response in crayfish. J Neurophysiol 64:64–76

Kennedy D, Bruno MS (1961) The spectral sensitivity of crayfish and lobster vision. J Gen Physiol 44:1089–1102

Marshall NJ, Jones JP, Cronin TW (1996) Behavioural evidence for colour vision in stomatopod crustaceans. J Comp Physiol A 179:473–481

May HY, Mercier AJ (2006) Responses of crayfish to a reflective environment depend on dominance status. Can J Zool 84:1104–1111

McMahon A, Patullo BW, Macmillan DL (2005) Exploration in a T-maze by the crayfish *Cherax destructor* suggests bilateral comparison of antennal tactile information. Biol Bull 208:183–188

Merrick JR (1991) The biology, conservation and management of Australian freshwater crayfishes. Macquarie University, New South Wales

Moore PA (2007) Agonistic behavior in freshwater crayfish: the influence of intrinsic and extrinsic factors on aggressive encounters and dominance. In: Duffy JE, Thiel M (eds) Evolutionary ecology of social and sexual systems: crustaceans as model organisms. Oxford University Press, Oxford, pp 90–114

Patullo BW, Macmillan DL (2006) Corners and bubble wrap: the structure and texture of surfaces influence crayfish exploratory behavior. J Exp Biol 209:567–575

Patullo BW, Baird HP, Macmillan DL (2009) Altered aggression in different sized groups of crayfish supports a dynamic social behaviour model. App Anim Behav Sci 120:231–237

Sandeman DC, Varju D (1988) A behavioral-study of tactile localization in the crayfish *Cherax destructor*. J Comp Physiol A 163:525–536

Seebacher F, Wilson RS (2007) Individual recognition in crayfish (*Cherax dispar*): the roles of strength and experience in deciding aggressive encounters. Biol Lett 3:471–474

Skog M (2009a) Male but not female olfaction is crucial for intermolt mating in European lobsters (*Homarus gammarus* L.). Chem Senses 34:159–169

Skog M (2009b) Intersexual differences in European lobster (*Homarus gammarus*): recognition mechanisms and agonistic behaviours. Behaviour 146:1071–1091

Tibbets EA, Dale J (2007) Individual recognition: it is good to be different. Trends Ecol Evol 22:529–537

Van der Velden J, Zheng Y, Patullo BW et al (2008) Crayfish recognise the faces of fight opponents. PLoS One 3:e1695

Vannini M, Gherardi F (1981) Dominance and individual recognition in *Potamon fluviatile* (Decapoda, Brachyura): possible role of visual cues. Mar Behav Physiol 8:13–20

Wald G (1967) Visual pigments of crayfish. Nature 215:1131–1133

Zulandt-Schneider RA, Schneider RWS, Moore PA (1999) Recognition of dominance status by chemoreception in the red swamp crayfish, *Procambrus clarkii*. J Chem Ecol 25:781–794

Zulandt-Schneider RA, Huber R, Moore PA (2001) Individual and status recognition in the crayfish, *Orconectes rusticus*: the effects of urine release on fight dynamics. Behaviour 138:137–153

Chapter 4
Social Recognition in Hermit Crabs

Brian A. Hazlett

Abstract The types of social recognition shown by hermit crabs are reviewed. Three aspects of hermit crab behavioral ecology that are important in social recognition are discussed. First, movement patterns can increase the probability of repeated interactions between individuals, thus increasing the possibility of social recognition based on past experience. Second, the phenomenon of individuality and consistency in the execution of behaviors is a necessary feature for individual social recognition. And finally, the evidence for dominance hierarchies in hermit crabs and the linkage to social recognition are considered. The experimental evidence for social recognition in hermit crabs is reviewed. While most studies have demonstrated just binary or class recognition (e.g., familiar versus non-familiar), the work of Gherardi and coworkers provide good evidence for possible true individual recognition in the hermit crab *Pagurus longicarpus*. The special considerations arising from the use of gastropod shells for protection by hermit crabs are discussed as they relate to aspects of social recognition.

Introduction

The crustaceans called hermit crabs would not have a place in a volume about social recognition, if one considered what is implied by their common name. But hermit crabs do have a rich repertoire of social behaviors (Hazlett 1966) and the hermit crab *Pagurus bernhardus* was one of the first invertebrates to be examined for evidence of social recognition (Hazlett 1969). However, the methodology used in that 1969 paper was not sufficient to establish true individual recognition. Hermit crab behavior is strongly influenced by the use of a mobile shelter and the quality of the inhabited shell affects almost all aspects of hermit crab behavior

---

B.A. Hazlett (✉)
Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, USA
e-mail: bhazlett@umich.edu

L. Aquiloni and E. Tricarico (eds.), *Social Recognition in Invertebrates*,
DOI 10.1007/978-3-319-17599-7_4

including social interactions (Tricarico and Gherardi 2007; Tricarico et al. 2011). One type of social interaction, territoriality, in the strictness sense is not shown by any hermit crab but if one looks at the gastropod shell occupied as a mobile territory, than all species of hermit crabs are territorial and the search by crabs for a better "territory" is an ongoing aspect of hermit crab behavior that can certainly influence other aspects of their behavior including social recognition.

If we included the processes of sex recognition and kin recognition in the general idea of social recognition, hermit crabs would have a mixed score. Recognition by males of females, and discrimination of individual females that are ready to mate, has been widely reported and olfactory cues are often implicated (e.g., Hazlett 1996a; Goshima et al. 1998). On the other hand kin recognition appears to be unlikely in hermit crabs given the dispersal of planktonic larvae such that close kin are unlikely to be found very near each other. Of the various types of recognition, social recognition and in particular, individual recognition (Steiger and Müller 2008; Tibbetts et al. 2008), have been studied in hermit crabs the most.

This review will, in large part, be a review of recent work of Dr. Gherardi and her coworkers on social recognition because they have done the majority of the research directly addressing social recognition. By incorporating the work of others, I hope to increase the generality of the ideas put forth by Dr. Gherardi. In the first sections of this review I will address some general concepts in ethology and behavioral ecology that are either necessary conditions or at least increase the possibility of social recognition in hermit crabs (repeated interactions, individuality, and dominance hierarchies). I will then focus on recent work examining social recognition in hermit crabs.

Repeated Interactions

For natural selection to favor the ability of individual crabs to recognize signals from particular conspecific individuals, individuals must encounter other individuals repeatedly. This constraint was addressed by Gherardi et al. (2012a) in their seminal review and they mentioned one situation where individual hermit crabs would interact repeatedly, namely interactions at a gastropod predation site. This occurs when a gastropod snail is being eaten by a predatory gastropod and an empty shell will result from the predation. One of the hermit crabs at the site will have access to the new shell and a series of shell switches can take place among the other individual crabs gathered at the site. The hermit crabs gathered at the predation site interact repeatedly for a number of hours or even several days (McLean 1973; Hazlett 1979), establishing an apparent dominance hierarchy with the "alpha" crab in the location where the new empty shell is most likely to appear. Interactions and multiple shell changes at a predation site can be either intraspecific or interspecific (Hazlett et al. 1996). It is conceivable that crabs could have repeated interactions with individuals of other species as they fight via visual displays for the best positions near the predation activity, thus recognition of individuals of other species is a possibility.

Another type of event that can facilitate repeated interactions among individual hermit crabs is their shell exchange behavior. In some species it has been reported that a shell exchange attempt (one crab attempting to obtain the shell inhabited by another crab) attracts other crabs to the site (Rittschof 1980). Numbers of crabs gather around the interacting pair and numerous agonistic interactions occur. While these “scrums” (Hazlett and Rittschof 1997) do not appear as organized as the interactions of crabs at a predation site and they do not appear to last as long as predation sites, repeated interactions between individuals can occur.

In addition to interactions at a predation site or shell exchange attempt, individual hermit crabs have the opportunity to interact repeatedly under other circumstances because their patterns of daily movements keep them near each other. The Caribbean species *Clibanarius tricolor* and *Pagurus miamensis* both aggregate in large clusters of conspecific individuals every day (following dispersal at night) and they orient, by odors from groups of conspecific individuals, to the same group day after day (Hazlett 1966). These groups can be large but repeated individual interactions are possible. Clustering also occurs in the Mediterranean species *Clibanarius erythropus* (Gherardi and Benvenuto 2001). A similar pattern of repeated interactions can occur in the Hawaiian species *Calcinus elegans*, where individuals stay in the same small tide pool for at least 4–7 days, when the crabs occupy certain species of shells (Hazlett and Bach 2009). Similarly, individuals of *Calcinus hazletti* can be found on coral reefs within a few cm of the same location and other marked individuals for at least 3–4 days in a row (Hazlett and Bach, unpublished results of mark-recapture studies). In general, crabs occupying the high intertidal often cluster together at low tide (Gherardi and Vannini 1993) and have the opportunity for repeated interactions among individuals.

It would appear that for a number of species of hermit crabs, movements result in crabs returning to the same location on a daily basis and thus repeated interactions between individuals could occur. In other species, this does not appear to be the case. For example, the daily movements of *Clibanarius vitattus* in North Carolina are quite extensive (individual crabs move many meters daily) and marked individuals do not end up near the same marked individuals very often (Hazlett 1981). If repeated interactions between individuals are a prerequisite for natural selection favoring the capabilities (both sending and receiving signals identifying individuals) necessary to show individual recognition, we can predict which species are more likely to show social recognition (including individual recognition) by knowing something about their patterns of daily movement.

Individuality

It would seem obvious that for hermit crabs to show social recognition, and especially individual recognition, there should be both differences among individuals in some features detectable by receivers and consistency in those differences. Crabs must show differences in some features if other individual crabs are to detect and react to those differences. And unless crabs are to some degree consistent in their behavioral tendencies, social interactions that include responses to differences in behavioral tendencies should not occur. It may not be critical for social recognition that animals show behavioral syndromes (behaving with similar ranks in the execution of different behaviors), but consistency in at least some behaviors is critical. While some workers have used the term "animal personalities" (see Bergmuller and Traborsky 2010) to indicate that there are consistent differences among individuals, I prefer the non-anthropomorphic term individuality.

While there have been a number of recent studies demonstrating individuality (and behavioral syndromes) in a number of species, there are relatively few such studies involving hermit crabs (Gherardi et al. 2012b). Briffa and coworkers (Briffa et al. 2008; Briffa and Twyman 2011) have shown that individuals of *P. bernhardus* differ from one another in the tendency to execute certain behavior patterns and are consistent in these differences across environmental conditions. However, some aspects of individual consistency in *P. bernhardus* were affected by temperature (Briffa et al. 2013), that is, the degree of consistency can be affected by general environmental conditions. Hazlett and Bach (2012) examined the defensive responses of three species of Hawaiian hermit crabs and found that there were significant individual differences within species in the strength of those responses and that the ranks of crabs in one type of test correlated well with the ranks in a second type of test (i.e., crabs showed behavioral syndromes). However, there was evidence of individuality (and behavioral syndromes) in only two of the species, *Calcinus laevimanus* and *C. elegans*. In the third species, *Calcinus haigae*, there were no significant differences among individuals in the strength of their responses to cues indicating increased predation risk. We can speculate that *C. haigae* is different because it appears to be in very well-fitting shells in nature. It seems clear that we can predict that social recognition and individual recognition would be more likely in individuals of *P. bernhardus*, *C. laevimanus* and *C. elegans* than in individuals of *C. haigae*.

Dominance Hierarchies

When a set of individuals interact repeatedly and there is a predictable winner in agonistic interactions with one animal winning over all others, a "beta" animal winning over all animals except the most dominant, and so on to the omega animal which loses to all others in the group, this is called a dominance hierarchy. In a classical dominance hierarchy the intensity of agonistic interactions decreases over time as individuals presumably recognize each other and retreat from one another without executing the strong displays used in the initial interactions establishing the hierarchy. Social inertia can also contribute to the stability see in established hierarchies. The hermit crab *Pagurus pollicaris* appears to form dominance hierarchies as they gather around a snail predation site both in the field (McLean 1973) and in the laboratory (Hazlett 1979). However, while the linear order of dominance is quite strong, the intensity of agonistic interactions did not decrease over time so one could question whether individuals of *P. pollicaris* are recognizing one another based on past interactions or simply reliably reacting to behavioral cues shown by other individuals. That is, an ordered arrangement of dominance could occur without individuals recognizing other individuals based on past interactions. The observations of Gherardi and Atema (2005a) showed that individuals of *Pagurus longicarpus* recognize group members after initial interactions, even before a stable hierarchy is established. However, the recognition reported by Gherardi and Atema (2005b) is binary (familiar versus unfamiliar individuals) rather than individual recognition in the strict sense.

Evidence for Social Recognition in Hermit Crabs

While my 1969 paper on *P. bernhardus* may have been the first to try to examine social recognition in crustaceans, the methodology used was not sufficient to conclude that individual recognition occurs in hermit crabs, and thus the use of quotation marks around the word "individual" in the title of that paper. Crabs that had been repeatedly interacting with one another for a week did interact differently with a "stranger" that was introduced on the last day of observations. Thus individuals of *P. bernhardus* did appear to recognize the class "non-group member" or "unfamiliar" but not necessarily a particular individual.

The recognition of two or more classes of individuals has been termed binary recognition (Boal 1996), and has been reported in the hermit crab *P. longicarpus* Gherardi and Tiedemann (2004a, b). They recorded the frequency of behavior patterns executed by focal individuals when those crabs were exposed either to just chemical cues, just visual cues, or both visual and chemical cues from familiar and unfamiliar conspecifics. The focal crabs clearly differentiated between the classes "familiar" and "unfamiliar" thus showing binary recognition. Moreover, crabs discriminated more clearly using olfactory cues than when using just visual cues. Of course the importance of chemical cues in the behavior of aquatic organisms in general is well known, including the Paguroidea (Gherardi and Tricarico 2011). In addition, Gherardi and Tiedemann (2004a, b) demonstrated that individuals of *P. longicarpus* showed self-recognition, responding differently to self-odor compared to odors from other familiar conspecifics. Multimodal recognition has been reported in other crustaceans (Crook et al. 2004; Aquiloni and Gherardi 2010) thus it is not surprising that hermit crabs may use sensory modalities in addition to olfaction in their social interactions.

The ability of hermit crabs to recognize individuals in the strict sense was tested most critically by Gherardi et al. (2005). Working with *P. longicarpus* they compared the behavior of focal individuals (the "receivers" of potential chemical signals) to two familiar individuals and to two unfamiliar individuals. The two crabs in each of the categories (familiar and unfamiliar) occupied different qualities of shell. In the tests with both classes of "senders", individual *P. longicarpus* differentiated between self-odor and non-self-odor, as shown by Gherardi and Tiedemann (2004a, b). Receivers did not differentiate between the two unfamiliar individuals occupying shells of different qualities. However, when the two senders were both familiar to the focal crab, that focal crab responded differently to the two individuals. Moreover, when the senders were placed in shells of different qualities than they inhabited when they first interacted with the focal animals, the discrimination of familiar individuals by the focal crab was no longer shown. That is, individuals of *P. longicarpus* were able to use chemical cues to recognize both individual crabs and something about the quality of the shell which each of the two familiar crabs occupied. In the Gherardi et al. (2005) study, it appears that what could be termed possible true individual recognition occurs. It remains unclear whether crabs were responding to any chemical cues from the shells themselves or to some chemical or chemicals given off by a hermit crab when it is occupying a shell of a particular quality.

In their review, Gheradi et al. (2012a) rightfully question if senders will always profit from identifying themselves. The phenomenon of shell exchanges in hermit crabs may provide a reason for identification. Shell exchanges are energetically expensive for the initiator (Mowles et al. 2010) and dangerous for both crabs given that predators may be attracted to the interaction. In the case of hermit crabs involved in a shell exchange attempt, there could be special complications, which derive from the fact that the "quality" of a particular shell varies with the size of the crab. The signals from the non-initiator crab presumably indicate something about that crab and what the quality of the shell is to that crab. There is a separate piece of information about how good the shell will be to the other crab (the initiator/aggressor) involved in the shell exchange. The advantage to the sending crab (the non-initiator in a shell exchange) is that the signal should indicate to the initiating crab how resistant the non-initiating crab will be to leave its current shell and this information may deter some interactions by a potential initiator (Hazlett 1996b). Initiating crabs (Hazlett 1996b) appeared to select shells occupied by other crabs that were not only better for them in size, but that were not particularly good for the non-initiator occupying them. It would also be advantageous to potential initiators to not repeatedly engage in shell exchange behavior with individuals that will not exchange shells with them assuming the initiators could identify such individuals (as long as they are in the same-quality shell, Gherardi et al. 2005). This avoidance of executing behaviors when success of shell exchange is low is similar to the avoidance of shells with the entrance blocked based upon past experience (Jackson and Elwood 1989). It should be noted that there are advantages to social recognition in shell exchange behaviors whether the crabs appear to be following the negotiations model (Hazlett 1996b) or aggression model (Briffa et al. 1998) of shell exchange.

In their summary of the properties of social recognition systems, Gherardi et al. (2012a) listed a number of potential properties of social recognition systems, in particular true individual recognition, and outlined the extent to which those properties have been demonstrated in hermit crabs. Of the 8 properties, 6 have been demonstrated in hermit crabs, primarily for *P. longicarpus*. One property is compatibility of TIR (True Individual Recognition) with the social system of the study organisms. In this review, I have added some aspects of hermit crab social systems that would increase the occurrence of repeated interactions and thus the possibility of TIR. A second property is adaptive value of the TIR and I have mentioned a possible additional feature of hermit crab interactions (shell exchange) that may increase the adaptive value of individual recognition. The other four properties listed by Gherardi et al. (2012a) that have been demonstrated in hermit crabs were compatibility of the TIR system with receiver's physiology, association of the TIR system with the receiver's experience, plasticity of templates and matching, and sender specificity of the receiver's actions. The two properties that Gherardi et al. (2012a) felt have not been demonstrated for hermit crabs both involve the signature cues utilized (specificity of signature cues and inter-individual variation of signature cues). Signature cues refer to the signals that are used by a receiver to identify individuals. Almost all published reports on social recognition in hermit crabs suggest that the cues will be chemical in nature, but the chemical identity of those cues and the question of specificity in the cues will require additional research. Variation in signature cues also needs to be addressed explicitly once the class of chemicals used as signature cues has been identified.

In conclusion, as the methodologies developed by Gheradi and co-workers are applied to other species of hermit crabs, we can begin to look at questions of the effects of differences in ecology on social recognition and look for phylogenetic patterns. Both of these lines of inquiry will of course require testing taxa in addition to model organisms such as *P. longicarpus* and *P. bernhardus*.

References

Aquiloni LF, Gherardi F (2010) Crayfish females eavesdrop on fighting males and use smell and sight to recognize the identity of the winner. Anim Behav 79:265–269

Bach CE, Hazlett BA (2009) Shell shape affects movement patterns and microhabitat distribution in the hermit crabs *Calcinus elegans*, *C. laevimanus* and *C. latens*. J Exp Mar Biol Ecol 382:27–33

Bergmuller R, Traborsky M (2010) Animal personality due to social niche specialization. Trends Ecol Evol 25:504–511

Boal JG (1996) Absence of social recognition in laboratory-reared cuttlefish, *Sepia officinalis* L. (Mollusca: Cephalopoda). Anim Behav 52:529–537

Briffa M, Bridger DP, Biro PA (2013) How does temperature affect behavior? multilevel analysis of plasticity, personality and predictability in hermit crabs. Anim Behav 86:47–54

Briffa M, Elwood RW, Dick JTA (1998) Analysis of repeated signals during shell fights in the hermit crab *Pagurus bernhardus*. Proc R Soc Lond B 265:1467–1474

Briffa M, Rundle SC, Fryer A (2008) Comparing the strength of behavioural plasiticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. Proc R Soc Lond B 275:1305–1311

Briffa M, Twyman C (2011) Do I stand out or blend in? conspicuousness awareness and consistent behavioural differences in hermit crabs. Biol Lett 7:330–332

Crook R, Patullo BW, Macmillan DL (2004) Multimodal individual recognition in the crayfish *Cherax destructor*. Mar Freshw Behav Physiol 37:271–285

Gherardi F, Aquiloni L, Tricarico E (2012a) Revisiting social recognition systems in invertebrates. Anim Cogn 15:745–762

Gherardi F, Aquiloni L, Tricarico E (2012b) Behavioral plasticity, behavioral syndromes and animal personality in crustacean decapods: an imperfect map is better than no map. Curr Zool 58:567–579

Gherardi F, Benvenuto C (2001) Vlustering behavior in a Medierranean population of the hermit crab Clibanarius erythropus. Ophelia 55:1–10

Gherardi F, Atema J (2005a) Effects of chemical context on shell investigation behavior in hermit crabs. J Exp Mar Biol Ecol 320:1–7

Gherardi F, Atema J (2005b) Memory of social partners in hermit crab dominance. Ethology 111:271–285

Gherardi F, Tiedemann J (2004a) Chemical cues and binary individual recognition in the hermit crab *Pagurus longicarpus*. J Zool Lond 263:23–29

Gherardi F, Tiedemann J (2004b) Binary individual recognition in hermit crabs. Behav Ecol Sociobiol 55:524–530

Gherardi F, Tricarico E (2011) Chemical ecology and social behavior of Anomura. In: Breithaupt T, Thiel M (eds) Chemical communication in Crustaceans. Springer, New York, pp 297–312

Gherardi F, Tricarico E, Atema J (2005) Unraveling the nature of individual recognition by odor in hermit crabs. J Chem Ecol 31:2877–2896

Gherardi F, Vannini M (1993) Hermit crabs in a mangrove swamp: proximate and ultimate factors in the clustering of *Clibanarius laevimanus*. J Exp Mar Biol Ecol 168:167–187

Goshima S, Kawashima T, Wada S (1998) Mate choice by males of the hermit crabs *Pagurus filholi*: do males assess repieness and/or fecundity of females? Ecol Res 13:151–161

Hazlett BA (1966) Social behavior of the Paguridae and Diogenidae of Curaçao. Stud Fauna Curaçao 23:1–143

Hazlett BA (1969) Individual recognition and agonistic behavior in *Pagurus bernhardus*. Nature 222:268–269

Hazlett BA (1979) Individual distance in Crustacea: IV. Distance and dominance hierarchies in *Pagurus pollicaris*. Mar Behav Physiol 6:225–242

Hazlett BA (1981) Daily movements of the hermit crab *Clibanarius vittatus*. Bull Mar Sci 31:177–183

Hazlett BA (1996a) Reproductive behavior of the hermit crab *Clibanarius vittatus* (Bosc, 1802). Bull Mar Sci 58:668–674

Hazlett BA (1996b) Assessments during shell exchanges by the hermit crab, *Clibanarius vittatus*: the compleat negotiator. Anim Behav 51:567–573

Hazlett BA, Bach CE (2012) Does shell species occupied influence individuality and behavioural syndromes in the defensive behaviour of three Hawaiian hermit crabs? Mar Freshw Behav Physiol 45:111–120

Hazlett BA, Rittschof D (1997) Multiple mechanisms of resource acquisition in hermit crabs: scrums and odor-induced grasping. Crustaceana 70:68–74

Hazlett BA, Rittschof D, Bach CE (1996) Interspecific shell transfer by mutual predation site attendance. Anim Behav 51:589–592

Jackson NW, Elwood RW (1989) Memory of information gained during shell investigation by the hermit crab, *Pagurus bernhardus*. Anim Behav 37:529–534

McLean RB (1973) Direct shell acquisition by hermit crabs from gastropods. Experientia 30:206–208

Mowles SL, Cotton PA, Briffa M (2010) Whole-organism performance capacity predicts resource-holding potential in the hermit crab *Pagurus bernharduds*. Anim Behav 80:277–282

Rittschof D (1980) Chemical attraction of hermit crabs and other attendants to gastropod predation sites. J Chem Ecol 6:103–118

Steiger S, Müller JK (2008) 'True' and 'untrue' individual recognition: suggestion of a less restrictive definition. Trends Ecol Evol 23:355

Tibbetts EA, Sheehan MJ, Dale J (2008) A testable definition of individual recognition. Trends Ecol Evol 23:356

Tricarico E, Gherardi F (2007) The past ownership of a resource affects the agonistic behavior of hermit crabs. Behav Ecol Sociobiol 61:1945–1953

Tricarico E, Breithaupt T, Gherardi F (2011) Interpreting odours in hermit crabs: a comparative study. Estuar Coast Shelf Sci 91:211–215

Chapter 5
Social Behaviour and Recognition in Decapod Shrimps, with Emphasis on the Caridea

Solomon T.C. Chak, Raymond Bauer and Martin Thiel

Abstract Common in most aquatic environments, shrimps occur in a wide range of social associations with conspecific and other species, and express various levels of social recognition. We review the mechanisms and forms of social recognition in shrimps, emphasizing the Caridea. Most research has been conducted on Alpheidae, Hymenoceridae, Hippolytidae, Palaemonidae and Stenopodidae. The olfactory first and chemotactile second antennae are important in perceiving waterborne cues/pheromones and contact pheromones. Potential distance and contact pheromones have been strongly suggested by behavioural studies in several species and even tentatively identified in a few species. All forms of social recognition and interspecific communication have been documented in shrimps, including recognition by mate, size, rank, kin and individual. Given the diversity of ecology, mating and social behaviour, and the previous research on social recognition in caridean shrimps, this group is a promising productive model taxon for studies in animal communication.

S.T.C. Chak
Virginia Institute of Marine Science, College of William & Mary, 1346,
Gloucester Point, VA 23062, USA
e-mail: tchak@vims.edu

R. Bauer
Department of Biology, University of Louisiana, Lafayette, LA 70504-2451, USA
e-mail: rtbauer@louisiana.edu

M. Thiel (✉)
Facultad Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile
e-mail: thiel@ucn.cl

M. Thiel
Millennium Nucleus Ecology and Sustainable Management of Oceanic Island (ESMOI),
Coquimbo, Chile

M. Thiel
Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile

L. Aquiloni and E. Tricarico (eds.), *Social Recognition in Invertebrates*,
DOI 10.1007/978-3-319-17599-7_5

Introduction

Shrimps are ubiquitous crustaceans in most aquatic environments (Bauer 2004). They occur in a wide range of social associations with conspecifics and also with other species (Fig. 5.1). Associations may consist of a minimum of two individuals (typically male and female), groups of several individuals (Baeza et al. 2010), and even reach aggregations of hundreds or more in commercially important schooling species of pandalid carideans and dendrobranchiate shrimps. Snapping shrimps (Alpheidae) are also the only marine invertebrate taxon with species that live in large eusocial groups (up to several hundred individuals), which are dominated by one or several queen-like females (Duffy 1996, 2007).

Given the diversity of group-association patterns in animal taxa, it is not surprising that a wide range of social associations and behaviours are reported for caridean shrimps (Bauer 2007), for example, dominance hierarchy among males (Ra'anan and Cohen 1985; Correa et al. 2003), coordinated defense by colony members in eusocial shrimps (Tóth and Duffy 2005), and pair living (Seibt and Wickler 1979; Knowlton 1980; Bauer 2004; Wong and Michiels 2011; Baeza et al. 2013). Since some species are known or supposed to cohabit for long time periods with conspecifics, it is to be expected that various levels of conspecific recognition have evolved.

Herein we review the existing literature on recognition in decapod shrimps, with emphasis on carideans, the group in which social recognition has been best studied. We present examples of the principal communication patterns currently

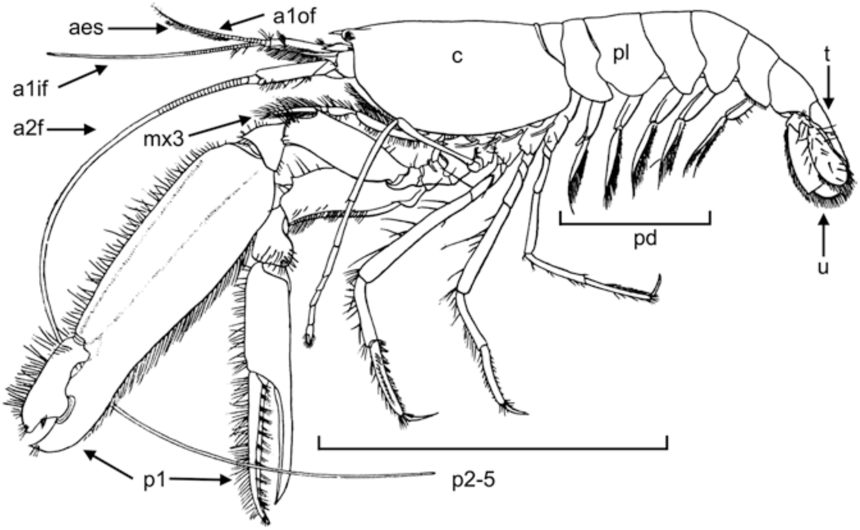


Fig. 5.1 External anatomy of a caridean shrimp, *Alpheus glaber*. The first pereopods (p1) are modified as specialized chelipeds. *a1if* inner flagellum of antennule (antenna 1); *a1of* outer flagellum of antennule; *a2f* flagellum of antenna (antenna 2); *aes* aesthetascs; *c* carapace; *mx3* third maxillipeds; *p1-5* pereopods (walking legs) 1-5; *pd* pleopod (swimming legs); *pl* abdominal pleuron; *t* telson; *u* uropod. Adapted from Holthuis (1955)

known in this group. We also highlight exciting cases for which more knowledge is urgently needed in order to understand the evolution of social behaviours in these beautiful crustaceans.

Shrimp Life Styles and Habitats

Most shrimps are medium-sized, being slightly larger than amphipods or isopods, but usually smaller than lobsters and many crabs. They have a well-developed abdomen and two pairs of chelipeds that can be morphologically quite variable (Fig. 5.1). These chelipeds may be used for food-processing, grooming, intra- and interspecific fights, and mating interactions. Females of caridean and stenopodidean shrimp species incubate their embryos under their abdomen and the eggs hatch into dispersing planktonic larvae in most species or benthic postlarvae or juveniles in some species (Bauer 2004).

Carideans are a taxonomically and ecologically diverse group (Bauer 2004) (Fig. 5.2). They are the most speciose of decapod shrimps, with at least

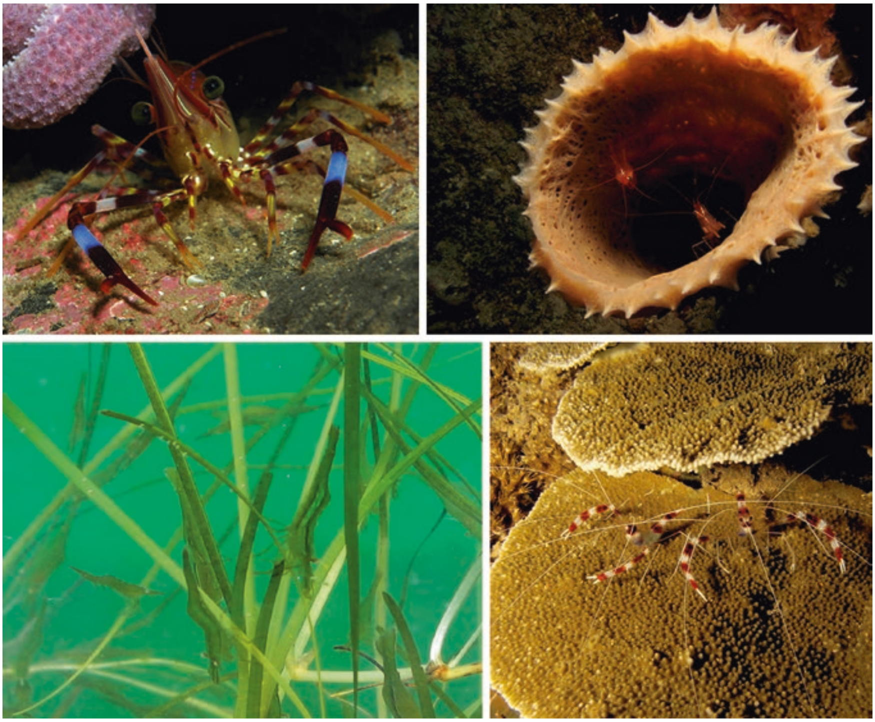


Fig. 5.2 Solitary caridean shrimp *Campylonotus vagans* (*upper left*), pair-living *Lysmata* sp. (*upper right*), gregarious *Hippolyte williamsi* (*lower left*), and monogamous stenopodidean shrimp *Stenopus hispidus* (*lower right*). Photographs courtesy of Dirk Schories (*upper left*) and Raphael Ritson-Williams (*upper* and *lower right*)

3400 species, compared to other shrimp taxa (Dendrobranchiata: 534 species; Stenopodidea: 70; DeGrave and Fransen 2011). Their geographic and bathymetric distributions are quite broad, as they occur in freshwater, estuarine and marine habitats. In the oceans, carideans occur at all depths and latitudes from pole to pole. They are an important component of neritic, pelagic, and deep-sea communities, occurring epibenthically over rocky, coral and soft sediments (sand and mud). Commercially important carideans, mainly pandalids and crangonids, are schooling species that move over soft-bottom marine habitats where they can be fished by trawling (Bergström 2000; Bauer 2004). Many carideans dig themselves into soft sediments during the day to emerge at night, and other species occupy more permanent burrows, often with a sexual partner. Carideans are a key component of seagrass and coral reef communities, and many species live in symbiotic associations with invertebrate hosts (Bruce 1976; Bauer 2004).

The Dendrobranchiata comprises the pelagic sergestoid and epibenthic penaeoid shrimps (Dall et al. 1990; Tavares and Martin 2010). The only known type of social organization in these shrimps is schooling, i.e., occurrence in large mobile aggregations. Penaeoids are subtropical and tropical species which are the most important component of the world's shrimp fisheries (Bauer 2004; Tavares and Martin 2010). The Stenopodidea is a small group with two major families, one (Stenopodidae) with species in shallow rocky and coral reef habitats in warm waters (Chockley et al. 2008; Goy 2010), while members of the other family (Spongicolidae) are associates of deep-water invertebrate hosts, especially hexactinellid (glass) sponges (Saito and Takeda 2003; Goy 2010). Most Stenopodidean species (for which such information is available) are reported to live as adults in male-female pairs (e.g. Saito et al. 2001; Goy 2010).

Mechanisms of Recognition

Decapod shrimps use waterborne (olfactory), contact or visual signals, or a combination of these, for social recognition. Specialized setae on the antennal (second antenna) flagella, third maxillipeds, and anterior pereopods are used to detect contact pheromones (Bauer 2011). Similar to other decapods (e.g. clawed lobsters, spiny lobsters, and crayfish; Aggio and Derby 2011; Breithaupt 2011), the first and second antennae are the main sites to perceive olfactory and contact signals (Fig. 5.1). Putative candidates for distance olfactory pheromone and contact pheromones have been identified in some species (Bauer 2011).

Waterborne cues are used by many shrimp species to obtain information about other individuals; in some species, the sender could even direct specific currents towards a receiver. For example, female *Hymenocera picta* produce a pheromone that is perceived by their male partners, which recognize their female partners among several shrimps (Seibt 1973). In the big-clawed snapping shrimp *Alpheus heterochaelis*, waterborne cues are important to differentiate between familiar and unfamiliar individuals (Ward et al. 2004). Transfer of these waterborne cues is facilitated by various behaviours of the emitting and receiving individuals. *Alpheus heterochaelis* produce various kinds of currents generated by the anterior appendages; some of these currents may be important in chemical communications (Herberholz and Schmitz 2001). A fast, strong, anterior-directed current is initiated after contact with a conspecific of either sex or with an interspecific shrimp. This current can likely reach the opponents' area of chemical perception. The frequency, duration, and range of the current are lower in encounters with interspecific individuals than in interactions with conspecifics. Moreover, the number of fast anterior gill currents is higher in winners than in losers of same-sex interaction, suggesting a role in hierarchy formation. Another current, the lateral gill current is produced by movements of the scaphognathites (the exopodites of the second maxillae), which is the most frequently observed current in *A. heterochaelis;* it has long intervals but has a short range and a low velocity. Lateral gill currents can likely improve the shrimps' ability to sense nearby chemical signals by constantly refreshing the area around its chemical receptors (Herberholz and Schmitz 2001).

The olfactory antennules and chemotactile antennae (first and second antennae) are important in perceiving the pheromones that permit differentiation of mates from non-mates, but the frequency of antennal exploration of other individuals may differ substantially between males and females, and also between different species (Vickery et al. 2012). In alpheid snapping shrimps, the antennae are used during initial contacts between individuals and the antennules are important for pair formation. During initial contacts, mutual antennulation (contact of one or both chemotactile antennae between two individuals) is more frequently observed in heterosexual than in homosexual interactions in both *Alpheus heterochaelis* and *A. normanni* (Nolan and Salmon 1970). Mutual antennulation often led to threat postures with open chela in homosexual interactions of both sexes. Successful pairing, however, may require olfactory function of the antennules. In *Alpheus edwardsii*, ablation of the antennae only slightly reduced heterosexual pairing frequency (Jeng 1994). However, ablation of the olfactory antennules (especially the outer antennular flagellum bearing the aesthetasc tufts) strongly reduced heterosexual pairing and increased homosexual pairing frequencies.

In *Macrobrachium rosenbergii*, the anatomy of the olfactory receptors, aesthetascs, and neural pathway to the brain have been examined (Kruangkum et al. 2013). Ablation of the lateral antennule (bearing aesthetascs) in males significantly reduced the mating success, but ablation of the antenna also caused a reduction in success. These results suggest that both olfaction (aesthetascs) and contact (antenna) may be involved in detection of olfactory or contact pheromones, respectively, and mate recognition in this species.

Potential candidates of distance and contact pheromones have been identified in two species of caridean shrimps, respectively. In the peppermint shrimp *Lysmata wurdemanni*, distance and contact pheromones operate together for successful copulation. Distance pheromones led to pre-copulatory approach and following behaviour for 5–120 min before the female moulted, while contact pheromones induced copulatory behaviour (Zhang and Lin 2004). Males tracked and located premoult females but not premoult males, presumably using distance pheromones specifically released by premoult females (but visual cues were not excluded) (Zhang and Lin 2006). “Washed” receptive females, which had insignificant amounts of distance pheromones, were not followed by males, but copulation still occurred after the male contacted the female with his antenna/antennules. Ablation of both antennae and antennules inhibited detection of distance and contact pheromones and resulted in no mating between males and receptive females. However, ablation of the outer flagella of the antennules inhibited only the detection of distance pheromones. A compound similar to the shore crab sex pheromone Uridine-di-phosphate was identified as the potential distance pheromone (Zhang et al. 2010). Aesthetascs on the outer flagella are likely the site of detection for distance pheromones, since they are innervated by olfactory receptor neurons and can possibly detect distance sex pheromones (Zhu et al. 2012b). Male-phase individuals of *L. wurdemanni* and several congeners have higher numbers of aesthetascs than those in the female (euhermaphrodite) phase, but this may be caused by delayed sex change in some males that attain larger sizes (Zhang et al. 2008; Zhu et al. 2012b). Moreover, the number of aesthetascs are also much higher in group living species (*L. wurdemanni* and *L. boggessi*) than in pair-living or low density species, suggesting the importance of aesthetascs in social interaction (Zhang et al. 2008; Zhu et al. 2012b). Despite the demonstration of waterborne pheromones, the production and source of these pheromones are still unknown. However, as in other crustaceans, waterborne signals are likely contained in urine released anteriorly through a pair of nephropores (Breithaupt 2011).

Contact signals/pheromones have been suggested in many shrimp recognition systems because contact by the antennae appears to initiate specific behaviours (e.g. snap or courtship). In the grass shrimp *Palaemonetes pugio*, males respond to postmoult parturial (sexually attractive) females only after touching them with the antennal flagella or the pereopods (Bauer and Abdalla 2001). Comparison of visual, tactile and behavioural cues as sexual signals pointed to the presence of a contact sex pheromone (Caskey and Bauer 2005) and further experiments identified glucosamine or a glucosamine-containing glycoproteins as the likely candidates (Caskey et al. 2009). Males can discriminate between reproductive (postmoult, parturial) and nonreproductive (nonparturial) females on the basis of contact chemoreception mediated through chemoreceptors on their antennae (Bauer 2011). Similar mechanisms are probably involved in mating behaviour and recognition of conspecifics in other aggregated and schooling species.

The contact recognition described for *Palaemonetes pugio* may be typical of shrimps with the pure-searching mating system (Wickler and Seibt 1981; Bauer 2004, 2011). These species generally live in aggregation with small males and larger females where frequency of contact is high. Females “hide” their reproductive condition as much as possible until after the moult, perhaps to prevent male harassment of females before they are receptive (Bauer and Abdalla 2001). Across caridean shrimps, at least 11 species are known to have pure-searching mating system (Correa and Thiel 2003) where the use of contact pheromones may play a crucial role in mate recognition. Pure search is the only known mating system for penaeoid shrimps (Bauer 1996), a group composed of aggregated or schooling species.

A potential mechanism for contact signal recognition is the ability of lectins to bind to specific carbohydrates on cell surfaces. Most studies on lectins in shrimps have focused on non-self-recognition for immune defense against microorganisms (Marques and Barracco 2000). Interestingly, N-acetyl-glucosamines (and mannose) are also found on the oocyte envelopes of *Rhynchocinetes typus*, which play an important role in spermatozoon recognition prior to the onset of penetration (Dupré et al. 2012). This suggests that similar chemical mechanisms may be employed for different recognition conditions in shrimps. Different sugar specificity and structural diversity have been observed for some species of crustaceans. In copepods, surface glycoproteins that can be targeted by lectins were shown to be important in mate recognition (Lonsdale et al. 1996, 1998). In grass shrimp *Palaemonetes pugio*, gas chromatography-mass spectrometry analysis of extracts from the cuticle also showed that cuticular composition of postmoult parturial females is very different from that of nonparturial females, males, and intermoult females (Caskey et al. 2009). The exact receptor and contact pheromone for social recognition have yet to be identified in caridean shrimps.

Felgenhauer and Abele (1982) suggested that also visual cues are involved in the recognition of mating partners in *Atya innocuous*. Similar observations have been reported by Díaz and Thiel (2004) who showed that in the rock shrimp *Rhynchocinetes typus* males recognize the presence of a reproductive female by visual cues from aggregations of males attempting to mate with the female. Although colouration is seldom sexually dimorphic in shrimps, Knowlton (1980) showed that males of *Alpheus armatus* had more colourful uropod spines (and larger snapping chelae) than females, and the mating system was polygynous. However, the mating system of the related *A. immaculatus*, from a nearby area with higher predation pressure, was more monogamous, and sexual dimorphism in colouration and chela size was absent and slight, respectively. Thus, visual cues in species with sexual differences in colouration may be important in mate recognition and should be investigated further. Visual cues also play a role in mate recognition in the stenopodidean *S. hispidus*, but chemical pheromones are much more important, with the strongest reaction when shrimps perceived both types of cues (visual and contact pheromone) in combination (Johnson 1969). Male *Alpheus heterochaelis* also modulate their behaviours in response to both pheromones and visual (open chela) signals (Hughes 1996a). Overall, visual signals have not received much investigation in caridean shrimps, but such cues may be important since shrimps have well developed compound eyes. However, chemical and contact pheromones may be a more efficient means of communication in complex habitats or for secretive and nocturnal species.

Familiar Recognition: Met Before?

As in other crustaceans, in some shrimp species the probability of meeting repeatedly is high. For example, this could be the case in burrow-living shrimps that defend burrows and forage in the vicinity of their home burrow, or in species that live in comparatively persistent aggregations, e.g. in crevices or on large hosts. Under these circumstances it may be advantageous for shrimps to recognize individuals they have interacted with before, for example to prevent potential injury by aggressive interactions. While recognition of familiar conspecifics has been described for various decapod crustaceans (e.g. Karavanich and Atema 1998; Gherardi et al. 2012; Tierney et al. 2013), this has not been explicitly tested for shrimps. Given that some shrimp species have evolved mechanisms to distinguish particular classes of individuals (see below) it is not unlikely that they also can recognize conspecifics they have met before.

There are intriguing reports that suggest that familiar recognition may not be uncommon among shrimps. For example, in the pair forming clown shrimp *Hymenocera picta* (Wickler and Seibt 1970), males guard their mates continually by fighting off rival males; observation of their behaviour suggests individual recognition ability (Seibt 1974; Seibt and Wickler 1972). In the cleaner shrimp *Lysmata debelius* from the tropical Pacific, an individual would spend significantly more time near its familiar mate than near a stranger in an experimental chamber (Rufino and Jones 2001).

In the big-clawed snapping shrimp *Alpheus heterochaelis*, an individual can discriminate between its mate and a stranger after separation for 24 h: the interaction with a stranger is more aggressive and less pairing behaviour was observed (Rahman et al. 2001). When pairing did occur between a resident female and a strange male, the latency to pairing was similar to pairing between familiar mates. However, when pairing occurred between a resident male and a strange female, the latency to pairing was much longer. Thus, there is potentially an interaction between sex and familiar recognition. Similar discrimination was also found between familiar and unfamiliar same-sex individuals based on waterborne cues alone (Ward et al. 2004).

Familiar recognition is also found in other decapod shrimps. In the stenopodidean banded shrimp *Stenopus hispidus* from Hawaiian reefs, mating pairs are thought to persist for repeated reproductive events despite frequent short-term separations at night. In encounters staged between previous mating partners, the individuals showed less aggression and courtship interactions than in encounters between heterosexual individuals that had never met before (Johnson 1969, 1977). Individuals can differentiate their mates from strangers, after having being separated for as much as 6 days (Johnson 1977).

Social Recognition

Social Environment

In some species, individuals appear capable of recognizing the social environment, translating this information into behavioural decisions or developmental processes. For example male-phase *Lysmata wurdemanni* delay sex change if they are maintained with female-phase (simultaneous hermaphrodite) individuals, which offers them ample opportunities to mate with the latter, which can breed both as male and female. Most likely males recognize the social environment via their successful mating investments (Baeza 2007a). The frequent and complex interactions within large groups may represent important stimuli for adaptive sex-change (Baeza and Bauer 2004). In *L. amboinensis*, which breed in pairs of simultaneous hermaphrodite individuals, Wong and Michiels (2011) observed that moulting frequency was higher in these pairs than in groups of 3 or 4 individuals—they suggested that the risk of cannibalism after moulting leads to moult suppression in groups. Moulting is necessary for simultaneous-hermaphrodite individuals to mate and spawn as females. In pairs, the risk of cannibalism is reduced because individuals take turns moulting and reproducing as females, and the individual acting as male does not attack and eat its pair partner.

In *Hymenocera picta* females reached sexual maturity much faster when maintained with males than when kept in isolation, but solitary females reached larger body sizes (Fiedler 2002). In male river shrimp *Macrobrachium rosenbergii*, maturation to the next sexually mature morphotype is accelerated when males of that morphotype are lacking from the social groups (Ra'anan and Cohen 1985). In the snapping shrimp *Alpheus angulatus*, males abandoned recently mated females more often when held in groups with female-biased sex ratio than in groups with equal sex ratio (Mathews 2002).

These reports suggest that shrimps are capable of detecting the size and composition of groups, resulting in group-dependent variations in moulting and development: individuals remain in (or proceed to) the developmental stage that is most favorable in the respective social environment. This is also indirect evidence that these species can recognize conspecifics of certain class in their social environment (e.g. sex and morphotype). The mechanisms of how social cues translate into physiological processes are not well understood.

Class-Level Recognition: Which Gang Do You Belong to?

Recognition of Conspecifics

In many marine systems, closely related species of caridean shrimps live within the same habitats. Consequently, it is important for individuals to discriminate against shrimps from other species. The antennae are commonly employed in recognition of conspecifics, most likely via chemical cues that can be transported with water currents (Herberholz and Schmitz 2001) or via contact chemicals on the body surface of the shrimps (Vickery et al. 2012).

The two peppermint shrimps *Lysmata wurdemanni* and *L. boggessi* are closely related, have partially overlapping distributions, but live in different habitats (Rhyne and Lin 2006). Both species are protandric simultaneous hermaphrodites in which juveniles mature as males (male phase) and later become simultaneous hermaphrodites that resemble and function as females (female phase) but have male function; we will refer to these two phases simply as MP and FP, respectively. Zhang et al. (2009) and Zhu et al. (2012a) found that reproductive isolation of the two species are due to differences in the molecular composition of sex pheromones leading to asymmetric mate recognition. MP *L. boggessi* rarely mate with FP *L. wurdemanni* because males cannot recognize the soluble sex pheromones from those FPs. In contrast, MP *L. wurdemanni* can recognize sex pheromones from moulted FP of *L. boggessi* and displayed pre-copulatory behaviour, but FP *L. boggessi* repelled MP *L. wurdemanni* likely by visual cues. Regardless of these FP behaviours, heterospecific matings between MP *L. wurdemanni* and FP *L. boggessi* occurred but only in the dark and not under light. Since moulting and mating of *L. wurdemanni* primarily occurred at night (Bauer and Holt 1998), it is unclear whether the observed asymmetric mate recognition between the two species translates into pre-zygotic isolation.

Eusocial colonies of *Synalpheus regalis* live in canals of marine sponges in the Caribbean, where the same species of sponge may be host to more than one *Synalpheus* species (Macdonald et al. 2006). Colony members reacted differently to conspecific nest-mates and congeners (Duffy 1996; Duffy et al. 2002). Conspecific nest-mates that were isolated overnight were accepted peacefully into the colony with very little aggression. In contrast, congeneric intruders induced elevated aggression and were sometimes killed. Immediately after antennal contact, residents usually snap at the interspecific intruder with its enlarged major chela (first pereopod), suggesting the presence of a contact chemical cue.

Many shrimps live in large, often mixed-species, aggregations or schools (Butler 1980; Bergström 2000). In large-bodied species, this behaviour makes them susceptible to fishing by trawling or other large netting devices, and thus considerable attention has been given to them by fisheries and aquaculture biologists. Although their social behaviour is little known, their mating behaviours have been studied sufficiently so that their mating system can be identified as “pure search” (Wickler and Seibt 1981; Bauer 1996, 2004). In this mating system, typical of species with small males and larger females, males are able to make frequent contact with females because of the aggregated or schooling behaviour of the species. Such aggregations are mobile and thus males have little opportunity to defend or guard a female. Recognition of conspecifics must be important to the maintenance of these large mixed-species schools so that the aggregation does not scatter below a critical density. Both contact and distance chemoreception may be involved in both remaining near conspecifics as well as recognition of an appropriate mating partner. Little work has been done in this area but should be a fruitful topic of future research.

Recognition of Potential Mates and Their Reproductive Status

In caridean shrimps, the female receptive period is always confined to a short period after moulting. Therefore, the selective pressure for males to detect a female when she is approaching a moult and receptivity to mating is high. Accordingly, many cases of recognition of potential mates and their reproductive status are documented in caridean shrimps, making use of chemical, contact and visual signals Table 5.1. Potential candidates of distance and contact pheromones have been identified in *Lysmata wurdemanni* and in *Palaemonetes pugio*, respectively (section "Mechanisms of Recognition").

Male and female *Hymenocera picta* were capable of distinguishing between non-moulting male and female conspecifics but only if they could touch them with their antennules (Seibt 1974). Males used distance pheromones to recognize recently moulted females (Seibt 1973, 1974). Small amounts of water conditioned by a moulting female seem sufficient to attract males from different parts of a large (0.7 m^2) holding tank (Seibt 1974). In experimentally formed pairs of *H. picta*, the physical distances between individuals decreased in heterosexual pairs as soon as both partners had attained sexual maturity, but the members of homosexual pairs maintained substantial distance to each other throughout the experiment (Fig. 5.3) (Fiedler 2002). Similarly in the freshwater shrimp *Atya innocuous*, the moulting females are recognized by males that are a few cm away from them (Felgenhauer and Abele 1982). In *Palaemon paucidens*, searching behaviour of males was only initiated when a postmoulted parturial female (with mature ovaries) or water conditioned by her was present (Kamiguchi 1972). In the latter case, some males would even attempt to copulate with a postmoult female without mature ovaries.

In the snapping shrimp *Alpheus angulatus* males can discriminate pre-moult and post-moult females based on at least waterborne chemicals. Using a y-maze apparatus (Fig. 5.4), Mathews (2003) exposed males to untreated water (control) against water coming from a tank holding a male or female shrimp that were either (i) pre-moult (<3 days from moulting), (ii) inter-moult (7 days after moulting or >3 days from moulting), or (iii) post-moult (<24 h after moulting). The differences in time spent in the treatment arm versus the control arm of the y-maze showed that males were only attracted to water coming from pre-moult females, but rejected water conditioned by inter-moult females and males (Table 5.2). Mate choice experiments further confirmed male preference for pre-moult females rather than post-moult females (Mathews 2003). Thus, males use waterborne chemicals to recognize females of different reproductive status and choose ones that offer higher reproductive return.

In another snapping shrimp species, *A. heterochaelis,* Hughes (1996b) found that individuals of both sexes do not differentiate chemical signals from either sex. However, chemical signals appear to modulate an individual's response to an open chela, an aggressive display of snapping shrimps. Without chemical signals, males responded to an opened chela as a function of the presented chela size aggressively by opening their chelae (Hughes 1996a). In comparison, males responded less aggressively to an open chela with female chemical signals, but more aggressively with male signals (Hughes 1996b). When exposed to male chemical signals, males responded equally aggressively to an open chela regardless of the presented chela size; but males reduced aggressiveness to smaller chelae when female signals or no signals were present. Females responded equally to open or closed chelae and were not affected by chemical signals. Therefore, male *A. heterochaelis* can

Table 5.1 Current knowledge of social recognition in Caridean shrimps and other decapod shrimps (*)

Family	Species	Comments	Social organization	Duration (h)	Mechanism	References
Class level recognition						
Alpheidae	*Alpheus angulatus*	Males discriminate pre-moult and post-moult females	Heterosexual pair	NA	Olfactory pheromones	Mathews (2003)
	Alpheus edwardsii	Ablation of the antennular flagella reduced paring	Heterosexual pair	NA	NA	Jeng (1994)
	Alpheus heterochaelis	Sex-specific chemical signals modulate an individual's response to an open chela	Heterosexual pair	NA	Olfactory pheromones and visual cues	Hughes (1996a)
		Females prefer larger or same-sized males than smaller males		NA	NA	Rahman et al. (2002, 2004)
		Shrimp recognize the dominance status of an opponent		NA	Olfactory pheromones	Obermeier and Schmitz (2003a, b, 2004)
	Synalpheus regalis	Colony member discriminate between nest-mate and foreign conspecific (could be interpreted as familiar recognition)	Eusocial	~10	Olfactory and contact pheromones	Duffy (1996), Duffy et al. (2002)
		Intruder discriminate between queen and other colony member		NA	NA	Duffy et al. (2002)
Atyidae	*Atya innocous*	Males recognize recently moulted, reproductive females	NA	NA	Olfactory pheromones and possibly visual cues	Felgenhauer and Abele (1982)

(continued)

Table 5.1 (continued)

Family	Species	Comments	Social organization	Duration (h)	Mechanism	References
Hymenoceridae	*Hymenocera picta*	Males recognize recently moulted females	Heterosexual pair	NA	Olfactory pheromones	Seibt (1973, 1974), Seibt and Wickler (1979)
		Males continually fight off rival males		NA	NA	Wickler and Seibt (1970)
Hippolytidae	*Lysmata pederseni*	Female-phase (FP) discriminate against male-phase (MP) individuals	Heterosexual pair	NA		Baeza (2010)
	Lysmata wurdemanni	MP recognize recently moulted FP	Aggregation	NA	Distance and contact pheromones	Zhang et al. (2009)
	Lysmata wurdemanni	FP preferentially mated with small rather than large mating partners		NA	NA	Baeza (2007b)
Palaemonidae	*Macrobrachium rosenbergi*	Female actively seek dominant males but avoid intermediate and small males	Aggregation	NA	NA	Ra'anan and Sagi (1985)
	Macrobrachium rosenbergi	Shrimps recognize the ranking of a conspecific		NA	NA	Barki et al. (1991)
	Palaemon paucidens	Water conditioned by receptive females induced male searching	Aggregation	30	Olfactory pheromones	Kamiguchi (1972)
	Palaemonetes pugio	Males discriminate between reproductive and non-reproductive females	Aggregation	NA	Contact pheromones	Bauer and Abdalla (2001), Caskey et al. (2009)

(continued)

Table 5.1 (continued)

Family	Species	Comments	Social organization	Duration (h)	Mechanism	References
Rhynchocinetidae	*Rhynchocinetes typus*	Female prefer dominant male	Aggregation	NA	Olfactory pheromones	Díaz and Thiel (2004)
Familiar recognition						
Alpheidae	*Alpheus heterochaelis*	Pair of mates and strangers behave differently	Heterosexual pair	24	NA	Rahman et al. (2001)
		Shrimp responded to reversed orientation of chemical cues from two familiar individuals (could be interpreted as true individual recognition)		0.05	Chemical cues	Ward et al. (2004)
	Synalpheus regalis	Colony member discriminate between nest-mate and foreign conspecific (could be interpreted as kin recognition)	Eusocial	~10	Olfactory and contact cues	Duffy (1996), Duffy et al. (2002)
Hymenoceridae	*Hymenocera picta*	Males continually fight off rival males		NA	NA	Wickler and Seibt (1970)
Hippolytidae	*Lysmata debelius*	Shrimp spend more time near its familiar mate than stranger	Heterosexual pair	NA	NA	Rufino and Jones (2001)
Stenopodidae*	*Stenopodus hispidus*	Pair of mates and strangers behave differently	Heterosexual pair	140	NA	Johnson (1977)
True individual recognition						
Alpheidae	*Alpheus heterochaelis*	Shrimp responded to reversed orientation of chemical cues from two familiar individuals (could be interpreted as familiar recognition)		0.05	Olfactory pheromones	Ward et al. (2004)

(continued)

Table 5.1 (continued)

Family	Species	Comments	Social organization	Duration (h)	Mechanism	References
Hymenoceridae	*Hymenocera picta*	Individual (heterosexual) partners recognize each other		NA	Olfactory pheromones	Seibt and Wickler (1972)
Hippolytidae	*Lysmata debelius*	Shrimp spend more time near its familiar mate than stranger	Heterosexual pair	NA	NA	Rufino and Jones (2001)
Stenopodidae*	*Stenopodus hispidus*	Pair of mates and strangers behave differently	Heterosexual pair	140	Unknown	Johnson (1977)

Durations are maximum times reported for the recognition; longer duration may not have been tested

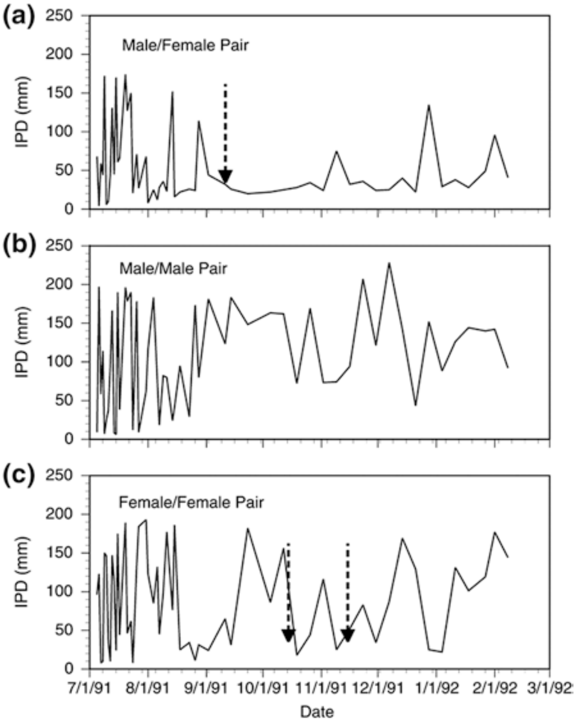


Fig. 5.3 Intrapair distance (IPD) for three pair types of naive juveniles throughout a year of lab observation. *Arrows* indicate the onset of maturity (appearance of secondary sex characters). IPD decreased in heterosexual pairs after female sexual maturity, but remained high in homosexual pairs. Adapted from Fiedler (2002)

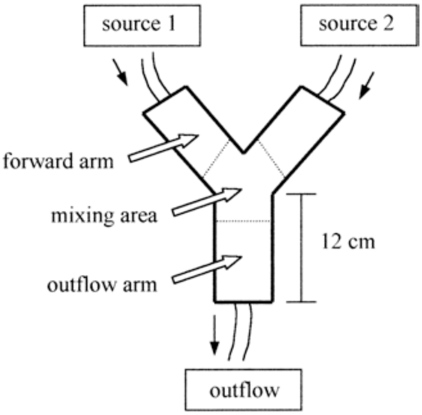


Fig. 5.4 A Y-maze apparatus to test for olfactory sex pheromones in *Alpheus angulatus. Solid arrows* indicate direction of water and pheromone flow. Times spent in the two forward arms were compared for significant differences. Adapted from Mathews (2003)

likely discriminate the sex of an individual by chemical signals, and modulate their responses according to the size of the opponent using visual cues.

In the eusocial snapping *Synalpheus regalis,* conspecific non-nest mate intruders contacted the queen (the only breeding female in the colony) more frequently than other colony members (a mix of non-reproductive females, males, and juveniles) in

Table 5.2 Testing for differences in time spent in the treatment arm (Source 1) against the control (Source 2)

Trial	Source 1	Source 2	*n*	Response	*p*
1	Intermolt female	Untreated	31	Negative	0.0052
2	Molted female	Untreated	30	–	0.4363
3	Premolt female	Untreated	32	Positive	0.0228
4	Intermolt male	Untreated	31	Negative	0.0002
5	Molted male	Untreated	28	–	0.1952
6	Premolt female	Untreated	29	–	0.3823
7	Untreated	Untreated	30	–	0.3210

Results show that *Alpheus angulatus* males can discriminate pre-moult females based on water-borne chemicals. Adapted from Mathews (2003)

lab experiments (Duffy et al. 2002). This also suggests that the reproductive female may produce pheromones that are detected by conspecifics.

Recognition of Size and Rank of Conspecifics

In many shrimp species there is substantial intrasexual variability in size and/or morphology. This opens the possibility that mates might choose among the individuals from the opposite sex. Moreover, when size or other phenotypic traits are correlated with fighting ability, rank-recognition may evolve (Gherardi et al. 2012). Potential physical cues include chela size in snapping shrimp (Hughes 1996b), chela colour and size differences between ontogenetic classes of *Macrobrachium rosenbergi* (Ra'anan and Cohen 1985), and strongly developed third maxillipeds and first chelae in dominant, male *Rhynchocinetes typus* (Correa et al. 2000).

Intersexual size-recognition has been observed in a few species. FP *Lysmata wurdemanni* preferentially mated with small rather than large mating partners (Baeza 2007b), but which stimuli they used to distinguish between mates (visual or chemical) is not known. Also, in *L. pedersoni*, large FP expelled small MP individuals from hosts, most likely because MP offered no return of female function (Baeza 2010). Small MPs were repeatedly struck with the third maxillipeds and/or the chelipeds.

In the big-clawed snapping shrimp *Alpheus heterochaelis*, which typically live in size-matched mating pairs, females would approach larger or same-sized males more often than smaller males and show more aggression (snapping) towards mates that are not size-matched (Rahman et al. 2002, 2004). This indicates that females recognize the sizes of a potential mate; such recognition is not observed in males. However, Obermeier and Schmitz (2003a) showed that both males and females may recognize the dominance status of an opponent. They exposed a loser in a first fight to (1) the winner of the first fight, (2) an unfamiliar winner, and (3) an inexperienced opponent for three consecutive trials. They found that losers showed immediate escape and less aggressive behaviour when encountering familiar and unfamiliar winners, but were more aggressive against an inexperienced opponent. At least for the first trial, this submissive behaviour can be explained by the recognition of a winner's dominant signals. In subsequent trials, the aggressiveness of the loser against an inexperienced opponent gradually decreased after consecutive losses, which suggests a reduction of fighting motivation. Obermeier and Schmitz (2003b) performed a further treatment using a loser with ablated lateral antennular filaments against a familiar winner. Operated losers did not escape and showed the same aggressiveness as in their first fights (Fig. 5.5). This shows that without olfactory reception, an individual cannot recognize the pheromones from a dominant winner, even with intact antennae to detect potential contact chemical pheromones. Further examination confirmed that unimodal chemoreceptors (aesthetascs) are unique to the lateral antennular filaments (Obermeier and Schmitz 2004).

Males of *Macrobrachium rosenbergi* have three ontogenetic stages with different mating strategies: blue claw (dominant), orange claw (intermediate), and small (sneaker) males (Ra'anan and Cohen 1985). After establishment of hierarchy between males of different ranks, aggressive acts decreased and submissive

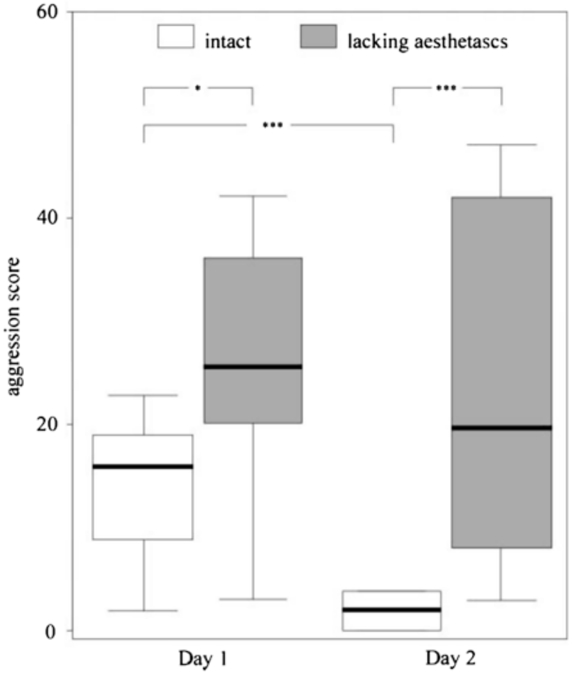


Fig. 5.5 Aggression scores of intact (aesthetascs present) and operated (aesthetascs ablated) *Alpheus heterochaelis* against a dominant opponent consecutively in two days. Intact shrimps recognized the dominant opponent in the encounter in the first day and reduced aggressiveness in the second encounter. However, shrimps with ablated aesthetascs did not recognize the dominant opponent and remain equally aggressive in the two encounters. Aggression scores were an estimate of fighting motivation involving the number of contact, snap, and fast anterior gill currents. Adpated from Obermeier and Schmitz (2003b)

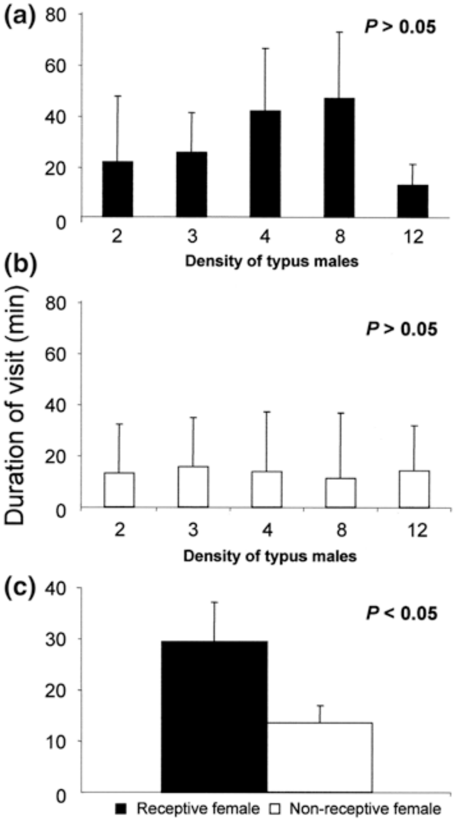


Fig. 5.6 Total visit duration of robustus males *Rhynchocinetes typus* to the **a** receptive female and **b** nonreceptive female in respective treatments (no significant differences between treatments). **c** Total visit duration of robustus males to the respective females after pooling among all treatments (significant differences between visits to respective females). *Bars* and *error bars* are mean and standard deviation. Adapted from Díaz and Thiel (2004)

acts increased between group members (Barki et al. 1991). This suggests that an individual may recognize the ranking of a conspecific and modify its behaviour to reduce possible injury.

An important form of mate recognition occurs in species with a “neighborhoods of dominance” mating system (Correa and Thiel 2003) in which the females approach the males which emit a pheromone (Bauer 2004). In *Macrobrachium australiense* and *M. rosenbergi*, when females are near the moult, they seek out the dominant male who would guard an approaching female until she moulted and mating occurred (Lee and Fielder 1982; Ra’anan and Sagi 1985). Similarly, in rock shrimp *Rhynchocinetes typus*, females select dominant males using chemical but not visual cues, despite the fact that dominant males (called robustus) are larger than and morphologically different from subordinate (typus) males. In contrast, robustus males do not locate a receptive female via chemical signals, but likely become aware of receptive females by visual cues created by agitated aggregations of small typus males around the receptive females (Díaz and Thiel 2004) (Fig. 5.6).

Recognition of Kin

In a broad sense, kin recognition describes the discrimination between kin and non-kin, irrespective of mechanisms or functions (Penn and Frommen 2010). In the eusocial snapping shrimp *Synalpheus regalis*, resident colony members responded to foreign conspecifics with more aggression and less contacts than to nest-mate conspecifics (Duffy et al. 2002). In cases where an intruder ignored repeated snaps by multiple residents, escalated responses of coordinated snapping were carried out by at least 60 % of the colony (Tóth and Duffy 2005). Nest-mates are likely full-siblings and juveniles usually remain within the natal colony (Duffy 1996). Therefore, colony members may be distinguishing between kin and non-kin and this can be viewed as kin recognition in a broad sense. Alternatively, this could merely be a case of familiar recognition, if foreign conspecifics are distinguished from nest-mates by cues that are independent of relatedness, such as, for example, the scent associated with the host sponge's secondary metabolites or microbial composition. It is also possible that kin recognition has evolved in other shrimps with direct development in which females cohabit for extended time periods with their offspring (e.g. Huguet et al. 2011; Guay et al. 2011), but to our knowledge this has not been studied.

True Individual Recognition: Are You Special?

Tibbetts and Dale (2007) defined true individual recognition as recognition in which all processes involved (cues, internal recognition template, and response) are individual specific, even when a receiver learned the unique cues of one individuals and subsequently treat that individual differently from others (Tibbetts et al. 2008). There have been arguments that this definition is too restrictive (Steiger and Müller 2008) or that it is operationally difficult to understand for invertebrates (Gherardi et al. 2012). Despite the different opinions, these authors all agreed that monogamous mate recognition can be considered true individual recognition.

Some shrimp species seem to have monogamous mate recognition that fits the individual recognition criteria. These species live together in persistent heterosexual pairs, and mating partners can recognize each other even when the females are not sexually receptive. This has been experimentally confirmed for the clown shrimp *Hymenocera picta* (Seibt 1973, 1974; Seibt and Wickler 1979), the cleaner shrimp *Lysmata debelius* (Rufino and Jones 2001) and the banded shrimp *Stenopus hispidus* (Johnson 1977) (Fig. 5.7). Moreover, pairs of the clown shrimp recognized each other and within a group of >10 individuals, males rapidly identify "their" females and quickly associate with them (Seibt and Wickler 1972). Members of a pair occasionally share food, but only after the individual that secured the food had been satiated (Seibt and Wickler 1979).

A property of true individual recognition defined by Gherardi et al. (2012) is that a receiver would behave differently to two or more individuals belonging to

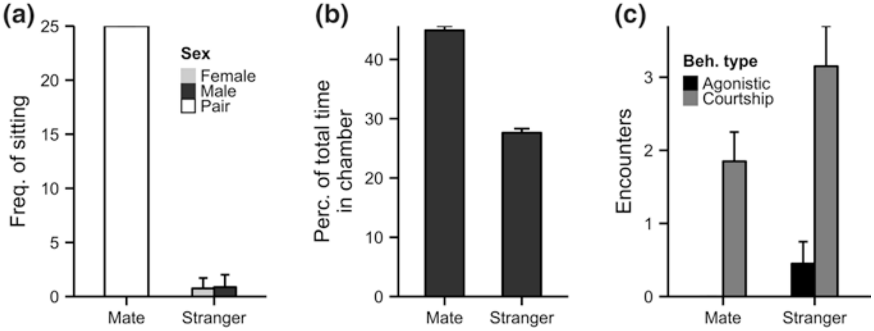


Fig. 5.7 Discrimination between mate and strangers in three monogamous decapods shrimps. **a** *Hymenocera picta*. Frequency of sitting with its mate or strangers in a mating pair of male and female (modified from Seibt 1974). Interactions with strangers is averaged from 8 individuals that were present in the same experimental tank and in which interactions were record separately for the male and female in the focal mating pair. **b** *Lysmata debelius*. Percentage of total time spent in each chamber where a mate or a stranger is present (modified from Rufino and Jones 2001). In a setup similar to a Y-maze, the test animals were allowed to choose from two chambers, each holding a mate or a stranger behind a filter, where chemical exchange and contact were allowed. **c** *Stenopus hispidus*. Frequencies of agonistic or courtship encounters between heterosexual mates and strangers within the first 5 min of contact after shrimps had been separated for two nights (modified from Johnson 1977). Note that courtship behaviour increased in encounters between strangers because it is used to establish new heterosexual pairing; this behaviour is generally lower between established pairs

the same familiar group. Ward et al. (2004) showed this in *Alpheus heterochaelis* by familiarizing a focal animal with the chemical cues of two size-matched, same-sex conspecifics for 3 h on two sides of a testing tank. Then they removed the sources of chemical cues and either repositioned them in the same (control) or opposite direction as before (treatment) for 30 min, followed by a final reposition of the cues for 30 min. Behaviours of the focal animal were compared between the first and last 30 min of the familiarization period, the control, and treatment periods. Antennal contact, leg poke and pull occurred more frequently in the experimental treatment than in the control, but did not differ between the two familiarization periods. The results show that the focal animal discriminated between two familiar chemical cues, thus being suggestive of true individual recognition.

Interspecific Associations and Communication

A number of snapping shrimps cohabit with other organisms. Many of these species commonly interact with their co-habitants, and sophisticated interspecific communication systems have been reported. For example, in the mutualistic, co-evolved partnership between gobies and alpheid shrimps, the shrimp maintains a continuous antennal contact with its goby partner; through tactile communication the goby notifies the shrimp of any danger with different behaviours modulated to the kind of threat, location and responses of the shrimp (Karplus and Thompson 2011). Shrimps are attracted to their associated goby species by waterborne chemical cues but not visual cues (Karplus 1981). Chemical cues are also found in symbiotic associations between some shrimp species and anemones (Guo et al. 1996), for example the ectosymbiotic association between a snapping shrimp and a feather star (VandenSpiegel et al. 1998).

A special case is the heterospecific association between two different species of alpheid shrimps, *Alpheus inca* and *Alpheopsis chilensis* (Boltaña and Thiel 2001). Heterosexual pairs of these two species cohabit in stable burrows in deeper layers of intertidal cobble beaches. Males and females of each species live in size-assorted pairs, and furthermore within quartets there is a positive relationship between the mean body size of *A. inca* pairs and that of *A. chilensis* pairs. Interestingly, even the reproductive status of the two heterospecific females within a quartet seems to be synchronized. These observations are suggestive of heterospecific communication but no details of the heterospecific behaviours and recognition between these two shrimp species are available (Boltaña and Thiel 2001).

In most cases, the heterospecific partners appear to live together without major agonistic interactions. However, in the association between the snapping shrimp *Betaeus lilianae* and the crab *Platyxanthus crenulatus*, and between *Alpheus salmoneus* and a *Trapezius* crab, aggressive behaviours by the crab towards the shrimp have been observed (Baeza et al. 2010; Vannini 1985). Interestingly, *A. salmoneus* has evolved to use submissive behaviour in shrimp–crab interaction to alleviate the crab's aggressive behaviour, so that it can share the habitat with the crab.

Conclusion and Outlook

Caridean shrimps are diverse in their ecology, mating and social behaviour, so it is not surprising that all types of social recognition are observed in this group. Among the various forms of recognition in caridean shrimps, mate recognition is best documented, in which potential distance and contact pheromones have been strongly suggested by behavioural studies in several species and even tentatively identified in a few species. With the previous work on these candidate pheromones and the documentation of social recognition in many species, similar pheromones could be more easily identified in other shrimp species. This would further advance the study of communication and social recognition in this group.

Snapping shrimps (Alpheidae) appear to have great potential for future research on social recognition. All three types of social recognition (familiar, class-level, and true individual recognitions) have been demonstrated in snapping shrimps (*Alpheus* and *Synalpheus*). In particular, *Synalpheus* is the only group among crustaceans in which eusociality has evolved, a social system in which terrestrial eusocial counterparts usually have complex modes of communication (Costa and Fitzgerald 1996).

Living in a group of close kin, in which individuals may perform different tasks (e.g. defense) and aggressiveness within the colony is rare and evolutionarily non-adaptive, might be a precursor to true individual recognition in eusocial *Synalpheus* species. Moreover, this group is ideal for comparative analysis since eusociality has evolved independently at least three times, and other species of *Synalpheus* express varying degrees of sociality ranging from pair-cohabitation (like many other alpheids) to communal living (Duffy et al. 2000). However, no formal experiment with any form of recognition has been performed in this genus and indications of mate recognition and kin recognition were only suggested from indirect evidence. Apart from eusocial species, many *Synalpheus* species live in multiple heterosexual pairs within the same sponge (communal species), in which the chance of encountering other conspecifics is expected to be high. This social system is intermediate between the typical pair-forming alpheids and the aggregation-forming species. No studies have yet explored the recognition system in species in relation to varying social structures in shrimps, and the genus *Synalpheus* could be an ideal model system to study the evolution of recognition in shrimps.

Among decapod shrimps, all *Exhippolysmata* and *Lysmata* species examined, and one species of *Parhippolyte*, have been shown to be protandric simultaneous hermaphrodites, in which shrimps are initially males and later turn into functional simultaneous hermaphrodites (Baeza et al. 2009; Braga et al. 2009; Onaga et al. 2012). Protandrous sequential hermaphroditism has been found in a number of caridean species (Bauer 2000; Chiba 2007), e.g. *Rhynchocinetes uritai* (Bauer and Thiel 2011). Simultaneous hermaphroditism and protandry in shrimps present a unique opportunity to investigate the ontogenetic development of sensory systems pertaining to mate recognition. Since females and males have different needs in terms of mate recognition or attraction, how do such systems co-exist in the same individual?

In conclusion, we have a basic understanding of social recognition in caridean and stenopodidean shrimps, but much remains to be learned. The diverse ecology, mating, sexual, and social systems of this group offer unique opportunities for studying the mechanisms and evolution of animal communication.

Acknowledgments MT was supported by the Chilean Millennium Initiative (grant NC120030). This paper is Contribution No. 3441 of the Virginia Institute of Marine Science, College of William & Mary.

References

Aggio J, Derby CD (2011) Chemical communication in lobsters. In: Breithaupt T, Thiel M (eds) Chemical communication in Crustaceans. Springer, New York, pp 239–256

Baeza JA (2007a) Male mating opportunities affect sex allocation in a protrandric-simultaneous hermaphroditic shrimp. Behav Ecol Sociobiol 61:365–370

Baeza JA (2007b) Sex allocation in a simultaneously hermaphroditic marine shrimp. Evolution 61:2360–2373

Baeza JA (2010) The symbiotic lifestyle and its evolutionary consequences: social monogamy and sex allocation in the hermaphroditic shrimp *Lysmata pederseni*. Naturwissenschaften 97:729–741

Baeza JA, Bauer RT (2004) Experimental test of socially mediated sex change in a protandric simultaneous hermaphrodite, the marine shrimp *Lysmata wurdemanni* (Caridea: Hippolytidae). Behav Ecol Sociobiol 55:544–550

Baeza JA, Schubart CD, Zillner P, Fuentes S, Bauer RT (2009) Molecular phylogeny of shrimps from the genus *Lysmata* (Caridea: Hippolytidae): the evolutionary origins of protandric simultaneous hermaphroditism and social monogamy. Biol J Linn Soc 96:415–424

Baeza JA, Farías NE, Luppi TA, Spivak ED (2010) Refuge size, group living and symbiosis: testing the "resource economic monopolization" hypothesis with the shrimp *Betaeus lilianae* and description of its partnership with the crab *Platyxanthus crenulatus*. J Exp Mar Biol Ecol 389:85–92

Baeza JA, Ritson-Williams R, Fuentes M (2013) Sexual and mating system in a caridean shrimp symbiotic with the winged pearl oyster in the Coral Triangle. J Zool 289:172–181

Barki A, Karplus I, Goren M (1991) Morphotype related dominance hierarchies in males of *Macrobrachium rosenbergii* (Crustacea, Palaemonidae). Behaviour 3–4:145–160

Bauer RT (1996) A test of hypotheses on male mating systems and female molting in decapod shrimp, using *Sicyonia dorsalis* (Decapoda: Penaeoidea). J Crust Biol 16:429–436

Bauer RT (2000) Simultaneous hermaphroditism in caridean shrimps: a unique and puzzling sexual system in the Decapoda. J Crust Biol 20(2):116–128

Bauer RT (2004) Remarkable shrimps: adaptations and natural history of the Carideans. University of Oklahoma Press, Norman

Bauer RT (2007) Hermaphroditism in caridean shrimps: mating systems, sociobiology, and evolution, with special reference to *Lysmata*. In: Duffy JE, Thiel M (eds) Evolutionary ecology of social and sexual systems: crustaceans as model organisms. Oxford University Press, New York, pp 232–248

Bauer RT (2011) Chemical communication in decapod shrimps: the influence of mating and social systems on the relative importance of olfactory and contact pheromones. In: Breithaupt T, Thiel M (eds) Chemical communication in Crustaceans. Springer, New York, pp 277–296

Bauer RT, Abdalla JH (2001) Male mating tactics in the shrimp *Palaemonetes pugio* (Decapoda, Caridea): precopulatory mate guarding vs. pure searching. Ethology 107:185–199

Bauer RT, Holt GJ (1998) Simultaneous hermaphroditism in the marine *shrimp Lysmata wurdemanni* (Caridea: Hippolytidae): an undescribed sexual system in the decapod Crustacea. Mar Biol 132:223–235

Bauer RT, Thiel M (2011) First description of a pure-search mating system and protandry in the shrimp *Rhynchocinetes uritai* (Decapoda: Caridea). J Crust Biol 31:286–295

Bergström B (2000) The biology of *Pandalus*. Adv Mar Biol 38:55–245

Boltaña S, Thiel M (2001) Associations between two species of snapping shrimp, *Alpheus inca* and *Alpheopsis chilensis* (Decapoda: Caridea: Alpheidae). J Mar Biol Assoc UK 81:633–638

Braga AA, Lopez Greco LS, Santos DC, Fransozo A (2009) Morphological evidence for protandric simultaneous hermaphroditism in the caridean *Exhippolysmata oplophoroides*. J Crust Biol 29:34–41

Breithaupt T (2011) Chemical communication in crayfish. In: Breithaupt T, Thiel M (eds) Chemical communication in Crustaceans. Springer, New York, pp 257–276

Bruce A (1976) Coral reef Caridea and commensalism. Micronesica 12:83–98

Butler TH (1980) Shrimps of the Pacific coast of Canada. Can Bull Fish Aquat Sci 202:1–280

Caskey J, Bauer R (2005) Behavioral tests for a possible contact sex pheromone in the caridean shrimp *Palaemonetes pugio*. J Crust Biol 25:571–576

Caskey JL, Hasenstein KH, Bauer RT (2009) Studies on contact sex pheromones of the caridean shrimp *Palaemonetes pugio*: I. Cuticular hydrocarbons associated with mate recognition. Invertebr Reprod Dev 53:93–103

Chiba S (2007) A review of ecological and evolutionary studies on hermaphroditic decapod crustaceans. Plankton Benthos Res 2:107–119

Chockley BR, St. Mary CM, Osenberg CW (2008) Population sinks in the Upper Florida Keys: the importance of demographic variation in population dynamics of the marine shrimp *Stenopus hispidus*. Mar Ecol Prog Ser 360:135–145

Correa C, Thiel M (2003) Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. Rev Chil Hist Nat 76:187–203

Correa C, Baeza JA, Dupré E, Hinojosa IA, Thiel M (2000) Mating behavior and fertilization success of three ontogenetic stages of male rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea). J Crust Biol 20:628–640

Correa C, Baeza JA, Hinojosa IA, Thiel M (2003) Male dominance hierarchy and mating tactics in the rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea). J Crust Biol 23:33–45

Costa JT, Fitzgerald TD (1996) The eusociality continuum revisited-reply. Trends Ecol Evol 11:472–473

Dall W, Hill B, Rothlisberg P, Staples D (1990) The biology of the Penaeidae. Adv Mar Biol 27:1–489

DeGrave S, Fransen C (2011) Carideorum catalogus: the recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). Zool Meded 85:195–588

Díaz ER, Thiel M (2004) Chemical and visual communication during mate searching in rock shrimp. Biol Bull 206:134–143

Duffy JE (1996) Eusociality in a coral-reef shrimp. Nature 381:512–514

Duffy JE (2007) Ecology and evolution of eusociality in sponge-dwelling shrimp. In: Duffy JE, Thiel M (eds) Evolutionary ecology of social and sexual systems: Crustaceans as model organisms. Oxford University Press, New York, pp 387–409

Duffy JE, Morrison CL, Rios R (2000) Multiple origins of eusociality among sponge-dwelling shrimps (*Synalpheus*). Evolution 54:503–516

Duffy JE, Morrison CL, Macdonald KS (2002) Colony defense and behavioral differentiation in the eusocial shrimp *Synalpheus regalis*. Behav Ecol Sociobiol 51:488–495

Dupré E, Gómez D, Araya A, Gallardo C (2012) Role of egg surface glycoconjugate in the fertilization of the rock shrimp *Rhynchocinetes typus* (Milne-Edwards, 1837). Lat Am J Aquat Res 40:22–29

Felgenhauer BE, Abele LG (1982) Aspects of mating behavior in the tropical freshwater shrimp *Atya innocous* (Herbst). Biotropica 14:296–300

Fiedler GC (2002) The influence of social environment on sex determination in harlequin shrimp (*Hymenocera picta*: Decapoda, Gnathophyllidae). J Crust Biol 22:750–761

Gherardi F, Aquiloni L, Tricarico E (2012) Revisiting social recognition systems in invertebrates. Anim Cogn 15:745–762

Goy JW (2010) Infraorder Stenopodidea Claus 1872. In: Schram FR, von Vaupel Klein JC (eds) Treatise on zoology-anatomy, taxonomy, biology. The Crustacea, volume 9 part A Eucarida: Euphausiacea, Amphionidacea, and Decapoda (partim). Leiden, Netherlands, pp 215–265

Guay C, Sainte-Marie B, Brêthes J-C (2011) Strong maternal effects and extreme heterogeneity of progeny development in the caridean shrimp *Sclerocrangon boreas* (Crangonidae). Mar Biol 158:2835–2845

Guo C-C, Hwang J-S, Fautin DG (1996) Host selection by shrimps symbiotic with sea anemones: a field survey and experimental laboratory analysis. J Exp Mar Biol Ecol 202:165–176

Herberholz J, Schmitz B (2001) Signaling via water currents in behavioral interactions of snapping shrimp (*Alpheus heterochaelis*). Biol Bull 201:6–16

Holthuis LB (1955) The recent genera of the caridean and stenopodidean shrimps (Class Crustacea, Order Decapoda, Supersection Natantia) with keys for their determination, vol 26. Zoologische verhandelingen. Brill, Leiden

Hughes M (1996a) The function of concurrent signals: visual and chemical communication in snapping shrimp. Anim Behav 52:247–257

Hughes M (1996b) Size assessment via a visual signal in snapping shrimp. Behav Ecol Sociobiol 38:51–57

Huguet D, García Muñoz J, Raso García J, Cuesta JA (2011) Extended parental care in the freshwater shrimp genus *Dugastella* Bouvier, 1912 (Decapoda, Atyidae, Paratyinae). Crustaceana 84:251–255

Jeng M-S (1994) Effect of antennular and antennal ablation on pairing behavior of snapping shrimp *Alpheus edwardsii* (Audouin). J Exp Mar Biol Ecol 179:171–178

Johnson VR Jr (1969) Pair formation in banded shrimps *Stenopus hispidus*. Am Zool 6:534–535

Johnson VR Jr (1977) Individual recognition in the banded shrimp *Stenopus hispidus* (Olivier). Anim Behav 25:418–428

Kamiguchi Y (1972) Mating behavior in the freshwater prawn, *Palaemon paucidens*: a study of the sex pheromone and its effect on males. J Fac Sci Hokkaido Univ Ser VI Zool 18:347–355

Karavanich C, Atema J (1998) Individual recognition and memory in lobster dominance. Anim Behav 56:1553–1560

Karplus I (1981) Goby-shrimp partner specificity. II. The behavioural mechanisms regulating partner specificity. J Exp Mar Biol Ecol 51:21–35

Karplus I, Thompson AR (2011) The partnership between gobiid fishes and burrowing alpheid shrimps. In: Patzner R, Van Tassell JL, Kovacic M, Kapoor BG (eds) Biology of gobies. Science Publishers Inc, New Hampshire, pp 559–608

Knowlton N (1980) Sexual selection and dimorphism in two demes of a symbiotic, pair-bonding snapping shrimp. Evolution 34:161–173

Kruangkum T, Chotwiwatthanakun C, Vanichviriyakit R, Tinikul Y, Anuracpreeda P, Wanichanon C, Hanna PJ, Sobhon P (2013) Structure of the olfactory receptor organs, their GABAergic neural pathways, and modulation of mating behavior, in the giant freshwater prawn, *Macrobrachium rosenbergii*. Microsc Res Tech 76:572–587

Lee C, Fielder D (1982) Maintenance and reproductive behaviour in the freshwatre prawn *Macrobrachium australiense* Holthuis (Crustacea: Decapoda: Palaemonidae). Mar Freshw Res 33:629–646

Lonsdale D, Snell T, Frey M (1996) Lectin binding to surface glycoproteins on *Coullana* spp. (Copepoda: Harpacticoida) can inhibit mate guarding. Mar Freshw Behav Physiol 27:153–162

Lonsdale DJ, Frey MA, Snell TW (1998) The role of chemical signals in copepod reproduction. J Mar Syst 15:1–12

Macdonald KS, Rios R, Duffy JE (2006) Biodiversity, host specificity, and dominance by eusocial species among sponge-dwelling alpheid shrimp on the Belize Barrier Reef. Divers Distrib 12:165–178

Marques MRF, Barracco MA (2000) Lectins, as non-self-recognition factors, in crustaceans. Aquaculture 191:23–44

Mathews LM (2002) Tests of the mate-guarding hypothesis for social monogamy: does population density, sex ratio, or female synchrony affect behavior of male snapping shrimp (*Alpheus angulatus*)? Behav Ecol Sociobiol 51:426–432

Mathews LM (2003) Tests of the mate-guarding hypothesis for social monogamy: male snapping shrimp prefer to associate with high-value females. Behav Ecol 14:63–67

Nolan B, Salmon M (1970) The behavior and ecology of snapping shrimp (Crustacea: *Alpheus heterochaelis* and *Alpheus normanni*). Forma et Functio 2:289–335

Obermeier M, Schmitz B (2003a) Recognition of dominance in the big-clawed snapping shrimp (*Alpheus heterochaelis* Say 1818) part I: individual or group recognition? Mar Freshw Behav Physiol 36:1–16

Obermeier M, Schmitz B (2003b) Recognition of dominance in the big-clawed snapping shrimp (*Alpheus heterochaelis* Say 1818) part II: analysis of signal modality. Mar Freshw Behav Physiol 36:17–29

Obermeier M, Schmitz B (2004) The modality of the dominance signal in snapping shrimp (*Alpheus heterochaelis*) and the corresponding setal types on the antennules. Mar Freshw Behav Physiol 37:109–126

Onaga H, Fiedler GC, Baeza JA (2012) Protandric simultaneous hermaphroditism in *Parhippolyte misticia* (Clark, 1989) (Caridea: Hippolytidae): implications for the evolution of mixed sexual systems in shrimp. J Crust Biol 32:383–394

Penn DJ, Frommen JG (2010) Kin recognition: an overview of conceptual issues, mechanisms and evolutionary theory. In: Kappeler P (ed) Animal behaviour: evolution and mechanisms. Springer, Berlin, pp 55–85

Ra'anan Z, Cohen D (1985) Ontogeny of social structure and population dynamics in the giant freshwater prawn *Macrobrachium rosenbergii* (de Man). In: Wenner A (ed) Crustacean issues, vol 3: Crustacean growth: factors in adult growth. Balkema, Roterdam, pp 277–311

Ra'anan Z, Sagi A (1985) Alternative mating strategies in male morphotypes of the freshwater prawn *Macrobrachium rosenbergii* (De Man). Biol Bull 169:592–601

Rahman N, Dunham DW, Govind CK (2001) Mate recognition and pairing in the big-clawed snapping shrimp, *Alpheus heterochelis*. Mar Freshw Behav Physiol 34:213–226

Rahman N, Dunham DW, Govind CK (2002) Size-assortative pairing in the big-clawed snapping shrimp, *Alpheus heterochelis*. Behaviour 139:1443–1468

Rahman N, Dunham DW, Govind CK (2004) Mate choice in the big-clawed snapping shrimp, *Alpheus heterochaelis* say, 1818. Crustaceana 77:95–111

Rhyne AL, Lin J (2006) A western Atlantic peppermint shrimp complex: redescription of *Lysmata wurdemanni*, description of four new species, and remarks on *Lysmata rathbunae* (Crustacea: Decapoda: Hippolytidae). Bull Mar Sci 79:165–204

Rufino MM, Jones DA (2001) Binary individual recognition in *Lysmata debelius* (Decapoda: Hippolytidae) under laboratory conditions. J Crust Biol 21:388–392

Saito T, Takeda M (2003) Phylogeny of the family Spongicolidae (Crustacea: Stenopodidea): evolutionary trend from shallow-water free-living to deep-water sponge-associated habitat. J Mar Biol Assoc UK 83:119–131

Saito T, Uchida I, Takeda M (2001) Pair formation in *Spongicola japonica* (Crustacea: Stenopodidea: Spongicolidae), a shrimp associated with deep-sea hexactinellid sponges. J Mar Biol Assoc UK 81:789–797

Seibt U (1973) Sense of smell and pair-bond in *Hymenocera picta* Dana. Micronesica 9:231–236

Seibt U (1974) Mechanismen und Sinnesleistungen für den Paarzusammenhalt bei der Garnele *Hymenocera picta* Dana. Z Tierpsychol 35:337–351

Seibt U, Wickler W (1972) Individuen-Erkennen und Partnerbevorzugung bei der Garnele *Hymenocera picta* Dana. Naturwissenschaften 59:40–41

Seibt U, Wickler W (1979) The biological significance of the pair-bond in the shrimp Hymenocera picta. Z Tierpsychol 50:166–179

Steiger S, Müller JK (2008) 'True'and 'untrue' individual recognition: suggestion of a less restrictive definition. Trends Ecol Evol 23:355

Tavares C, Martin JW (2010) Suborder Dendrobranchiata Bate, 1888. In: Schram FR, von Vaupel Klein JC (eds) Treatise on zoology-anatomy, taxonomy, biology. The Crustacea, volume 9 Part A Eucarida: Euphausiacea, Amphionidacea, and Decapoda (partim). Leiden, Netherlands, pp 99–164

Tibbetts EA, Dale J (2007) Individual recognition: it is good to be different. Trends Ecol Evol 22:529–537

Tibbetts EA, Sheehan MJ, Dale J (2008) A testable definition of individual recognition. Trends Ecol Evol 23:356

Tierney A, Andrews K, Happer K, White M (2013) Dear enemies and nasty neighbors in crayfish: effects of social status and sex on responses to familiar and unfamiliar conspecifics. Behav Process 99:47–51

Tóth E, Duffy JE (2005) Coordinated group response to nest intruders in social shrimp. Biol Lett 1:49–52

VandenSpiegel D, Eeckhaut I, Jangoux M (1998) Host selection by *Synalpheus stimpsoni* (De Man), an ectosymbiotic shrimp of comatulid crinoids, inferred by a field survey and laboratory experiments. J Exp Mar Biol Ecol 225:185–196

Vannini M (1985) A shrimp that speaks crab-ese. J Crust Biol 5:160–167

Vickery R, Hollowell K, Hughes M (2012) Why have long antennae? Exploring the function of antennal contact in snapping shrimp. Mar Freshw Behav Physiol 45:161–176

Ward J, Saleh N, Dunham D, Rahman N (2004) Individual discrimination in the big-clawed snapping shrimp, *Alpheus heterochelis*. Mar Freshw Behav Physiol 37:35–42

Wickler W, Seibt U (1970) Das Verhalten von *Hymenocera picta* Dana, einer Seesterne fressenden Garnele (Decapoda, Natantia, Gnathophyllidae). Z Tierpsychol 27:352–368

Wickler W, Seibt U (1981) Monogamy in Crustacea and Man. Z Tierpsychol 57:215–234

Wong JW, Michiels NK (2011) Control of social monogamy through aggression in a hermaphroditic shrimp. Front Zool 8:30–37

Zhang D, Lin J (2004) Mating without anterior pleopods in a simultaneous hermaphroditic shrimp, *Lysmata wurdemanni* (Decapoda, Caridea). Crustaceana 77:1203–1212

Zhang D, Lin J (2006) Mate recognition in a simultaneous hermaphroditic shrimp, *Lysmata wurdemanni* (Caridea: Hippolytidae). Anim Behav 71:1191–1196

Zhang D, Cai S, Liu H, Lin J (2008) Antennal sensilla in the genus *Lysmata* (Caridea). J Crust Biol 28:433–438

Zhang D, Lin J, Hardege JD, Rhyne AL (2009) Reproductive isolation between two sympatric simultaneous hermaphroditic shrimp*, Lysmata wurdemanni* and *L. boggessi*. Mar Biol Res 5:470–477

Zhang D, Lin J, Harley M, Hardege JD (2010) Characterization of a sex pheromone in a simultaneous hermaphroditic shrimp, *Lysmata wurdemanni*. Mar Biol 157:1–6

Zhu J, Zhang D, Lin J (2012a) Asymmetric mating isolation between two caridean shrimp: *Lysmata wurdemanni* and *Lysmata boggessi*. J Shellfish Res 31:195–199

Zhu J, Zhang D, Lin J, Grace MS (2012b) Aesthetascs in *Lysmata* spp. shrimp: sexual dimorphism and relationship with social environments. Mar Biol 159:507–517

Chapter 6
Social Recognition in Amphipods: An Overview

Jan Beermann, Jaimie T.A. Dick and Martin Thiel

Abstract Many amphipod species occur in dense aggregations, cohabit with mating partners for long time periods, or live in family groups. Although this confers ample opportunities for social interactions among conspecifics, little is known about social recognition patterns in these species. Current research indicates that social recognition in amphipods is largely limited to mate and female-offspring recognition. In many amphipod species, the males are capable of assessing the reproductive status/quality of females and choose mates accordingly. While females of some species are capable of recognizing their own brood, in other species females seem to be indiscriminate towards their own or unrelated embryos. Some observations, however, suggest kin recognition within family units and even ranking of conspecifics seems to be likely. Central-place foraging has not been reported for amphipod families thus far, and also their potential for fortress defense is very limited. It thus appears that higher level

---

J. Beermann
Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research,
Biologische Anstalt Helgoland, Postbox 180, 27483 Helgoland, Germany
e-mail: jan.beermann@awi.de

J.T.A. Dick
Institute for Global Food Security, School of Biological Sciences,
Queen’s University Belfast, 97 Lisburn Road, Belfast BT9 7BL, Northern Ireland, UK
e-mail: j.dick@qub.ac.uk

M. Thiel (✉)
Facultad Ciencias del Mar, Universidad Católica del Norte,
Larrondo 1281, Coquimbo, Chile
e-mail: thiel@ucn.cl

J.T.A. Dick
Charles Darwin University, Darwin, NT 0909, Australia

M. Thiel
Millennium Nucleus Ecology and Sustainable Management of Oceanic Island (ESMOI),
Coquimbo, Chile

M. Thiel
Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile

L. Aquiloni and E. Tricarico (eds.), *Social Recognition in Invertebrates*,
DOI 10.1007/978-3-319-17599-7_6

social recognition may not have evolved in amphipods, although we recognize a lack of research in this area. Given their easy maintenance in laboratory cultures and technological advances in video recording and analysis, we believe that selected amphipod species could be ideal model organisms to study the evolution of social behavior.

Introduction

Amphipods often occur in dense aggregations (e.g. Aumack et al. 2011; Rigolet et al. 2012; Vitaliano et al. 2013) and frequent interactions among conspecifics can thus be expected. Courting individuals must recognize potential mates of their own species (Dick and Elwood 1992; Cothran et al. 2013) and distinguish between members of the same and the opposite sex (Thiel 2011a). Once the correct species has been identified, individuals might choose preferred mating partners, for example, based on moult stage, size and parasite status (Poulton and Thompson 1987; Dick and Elwood 1989; Thomas et al. 1996; Thiel 2011a, b). If mates stay together after fertilization, there might be a need for individual recognition. Similar to isopods (e.g. Linsenmair 2007), amphipods feature direct development and parents might care for their offspring after these are born (have emerged from the maternal brood pouch); in this case, the need for family recognition (parents and offspring mutually recognizing each other) might have evolved (Thiel 2007). In addition to such post-emergence juvenile care, pre-emergence brood care, such as egg retrieval following loss from the marsupium, is also facilitated by kin recognition in amphipods (Patterson et al. 2008).

All these social interactions require sensory and neuronal systems that permit exchange and processing of information between individuals (e.g. Wyatt 2011). While there are some suggestive observations, very few studies have rigorously examined whether and how individual amphipods distinguish conspecifics or might even recognize particular individuals. In the present overview, we provide examples for each applicable form of recognition described in Gherardi et al. (2012): mate and kin recognition as well as the evaluation of higher- and lower-ranking individuals. In each section, we first describe the best studied cases and then report examples that are highly suggestive of recognition but without observational or experimental evidence. We wish to emphasize upfront that little is known about social recognition in amphipods, but we hope that we will be able to convince readers that this group can be a fertile ground for exciting discoveries in the future.

Life Styles and Habitats

Amphipods inhabit all aquatic habitats from the deep ocean and hydrothermal vents to cold mountain springs and even terrestrial habitats (e.g. Barnard and Karaman et al. 1991; Väinölä et al. 2008). Many species are highly mobile, being constantly on the move in search of food and mates. For example, some pelagic amphipods form dense feeding swarms that continuously change shape, density and extension (Lobel and Randall 1986; Sheader et al. 2000). How coordination is maintained between the neighboring individuals in these dense swarms is not known at present but it is suspected that vision and mechano-reception might be involved (Ritz et al. 2011).

Scavenging amphipods roam above the seafloor in search of food: once they receive a chemical stimulus indicating nearby carrion, they rapidly track and follow the chemical cues to the food source (Sainte-Marie 1992; Premke et al. 2003). On large carcasses, hundreds and even thousands of scavenging amphipods will rapidly congregate in dense and voracious feeding aggregations, which might result in frequent intra- and interspecific interactions (e.g. Thurston 1979; Moore 1994; Moore and Wong 1995; Premke et al. 2006). Herbivorous amphipods move around between living macrophytes or plant detritus, i.e. they live in and on their food sources. Some species are widespread on their host-plants, and interactions are probably infrequent, while others form dense aggregations in favorable locations, where individuals are in continuous contact with conspecifics (e.g. Gunnill 1984; Duffy 1990).

Many amphipods also have a semi-sessile life style, inhabiting self-constructed tubes from which they capture suspended food particles, graze epiphytes and/or consume macroalgal or seagrass tissue on which they construct their tubes (e.g. Brawley and Adey 1981; Dixon and Moore 1997; McDonald and Bingham 2010). Other species excavate underground galleries in soft-bottoms where they consume organic matter that they sort out of the sediment (Atkinson et al. 1982). Tube- and burrow-dwellers usually cohabit only with mates and/or offspring in their domiciles, but, especially among the suspension-feeders in favorable feeding locations, there might be extraordinarily high densities of tubes, resulting in frequent intraspecific interactions.

Several authors have suggested gregariousness in amphipods (e.g. Drolet et al. 2013), but the underlying mechanisms and individual detection of conspecific aggregations is not well understood. Amphipods are also prey to a wide range of vertebrate and invertebrate predators, and it is thus not surprising that they adjust their behavior in response to predators (e.g. MacNeil et al. 1999; Wisenden et al. 2001). Some species aggregate when exposed to predator cues (Kullmann et al. 2008; Durieux et al. 2012), but it is not known how amphipods interact within these aggregations. In addition, such aggregations may rather be a predatory/scavenging response to such cues, as some amphipods such as *Gammarus* spp. are well known to be omnivorous and opportunistic in their feeding (MacNeil et al. 1997). When sensing the presence of a predator, some amphipod species shift their substratum preferences (Baumgärtner et al. 2003), or they are less inclined to form mating pairs during reproduction (Dunn et al. 2008; Ahlgren et al. 2011). Parasitism might also negatively affect the tendency of amphipods to aggregate (Durieux et al. 2012).

In dense aggregations, amphipods may aggressively interact with conspecifics (Van Tomme et al. 2012). Aggression may depend on the availability of resources and the conspecific densities within these aggregations. Furthermore, some amphipod species appear to be much more aggressive than others, even in closely related species (Dick et al. 1995; Van Tomme et al. 2012). Some adults can be aggressive towards juveniles and cannibalize these when food availability is limited (Duarte et al. 2010) and these effects may be reinforced at high densities (Wenngren and Ólafson 2002). However, the occurrence of filial cannibalism can also depend on the brooding status of individuals and may be reduced by juvenile avoidance behaviors (Lewis et al. 2010), with evidence of kin recognition reducing cannibalism of eggs (Patterson et al. 2008).

Signals and Communication Channels

Amphipods employ a wide variety of communication channels, but chemical cues are by far the most important in exchanging information between conspecifics (see Thiel 2011a and references therein). The specific substances used for communication are not well known, but molt hormones may play an important role in reproductive interactions. Perception of chemical stimuli happens via specific sensillae that are concentrated on the antennae, but can also take place on other body parts (Hallberg and Skog 2011).

Visual communication may also play a role in amphipod interactions, but to our knowledge this has not been specifically tested. Intriguing observations have been reported for an intertidal beach hopper, where dominant males may signal their status to smaller males and to females via color on their anterior appendages (Iyengar and Starks 2008). Acoustic communication appears unlikely, since amphipods do not seem to have a specific sensory system for mechanical stimuli (Enright 1962). However, a lateral line organ may allow for vibration detection in certain frequencies (Platvoet et al. 2007) and some structures were interpreted as stridulating ridges in some amphipod genera such as *Ericthonius* (e.g. Myers and McGrath 1984; Krapp-Schickel 2013) and *Photis* (e.g. Myers 2009).

Social Recognition

To date, there are no documented cases of familiar, true individual, or self-recognition in Amphipoda. Following the definitions provided by Gherardi et al. (2012), this overview therefore focuses on the few observed examples of class-level recognition among conspecifics (i.e. class assignment to, and distinction of individuals).

Mate Recognition

Amphipods are efficient in recognizing potential mates of their own species. They are able to discriminate amongst closely related species, even though interspecific mating pairs are occasionally observed (Kolding 1986; Dick and Elwood 1990; Cothran et al. 2013). In most of these experiments, males had direct access to congeneric females and consequently it cannot be determined if the cues that males use to recognize conspecifics are waterborne or contact chemicals. Females may also resist pairing advances from congeneric males more vigorously than those of conspecific males, thereby positively influencing the proportion of conspecific pairings (Cothran et al. 2013).

When offered waterborne cues in choice-experiments with conspecific females, males commonly show a strong preference for receptive females (Borowsky 1984, 1985a, b, 1991; Krång and Baden 2004). Most studies examined whether males can recognize females, but the choices of females have rarely been tested explicitly (see above and Iyengar and Starks 2008). Females held by a male in the precopulatory embrace usually pass through shorter intermolt periods than unguarded females (Kinne 1953, 1960; Galipaud et al. 2011), which seems to be controlled in *Gammarus* by the direct physical contact of the precopula (Kinne 1953).

Reproductive Quality and Conditions

Amphipod males are capable of assessing a number of parameters during courtship (e.g. reproductive quality of females, levels of intrasexual competition, necessary energy/time investment), allowing for maximal reproductive success. For example, *Gammarus* males make complex decisions in their evaluation of females before and during mate guarding. Female individuals are assessed and compared by body size, molt stage and brood pouch content and males even abort existing precopulae when encountering higher quality females (Fig. 6.1; Dunham 1986; Dunham et al. 1986; Dick and Elwood 1989, 1990; Dick 1992). Male assessment of female reproductive quality is also evidenced by more intense struggles for females close to molt, and hence ready for insemination (Fig. 6.2). Furthermore, *Gammarus* males can assess the degree of intrasexual competition within a population (overall sex ratio/male density, body size of competitors), reacting with longer lasting guarding behavior and/or

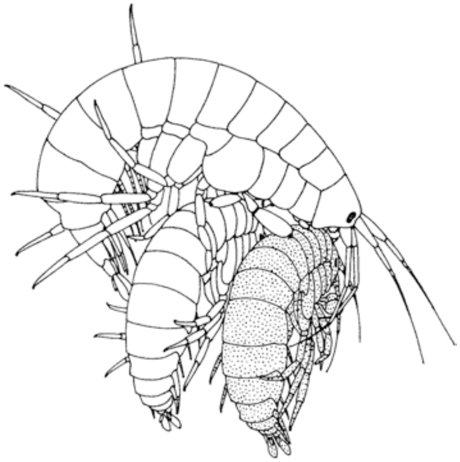
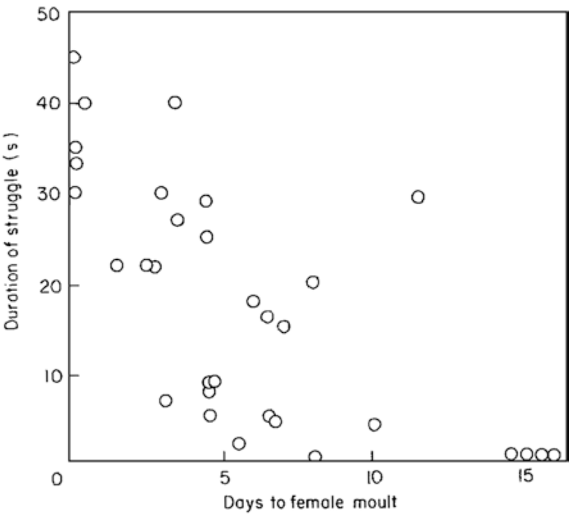


Fig. 6.1 Male *Gammarus pulex* have the ability to hold two potential precopula mates simultaneously, assess their relative reproductive potential, and retain the female that will yield the highest number of fertilizations per unit time of male investment (drawing modified after Dick 1992)

Fig. 6.2 Since female *Gammarus pulex* are assessed by the males as to their molt stage, males are more committed to engage in aggressive encounters as females get closer to their molt (after Dick and Elwood 1990)



guarding of females which require a longer time investment (Fig. 6.3; Dunham and Hurshman 1990; Iribarne et al. 1995; Dick and Elwood 1996). An assessment behavior by females seems to occur in the tube-dwelling *Jassa marmorata* Holmes, 1903. When reaching the terminal molt, *Jassa* males develop thumb-like protuberances on the 2nd gnathopods (see Sect. Ranking of Conspecifics). Although sexually mature already before this molt, thumbless males face a higher probability of getting evicted by females, whereas thumbed males are never attacked (Borowsky 1985a, b as '*Jassa falcata*'). Also, females of the highly territorial species *Dyopedos monacanthus* (Metzger, 1875) only tolerate adult or nearly adult males on their self-constructed "mud whips"/"masts" (Mattson and Cedhagen 1989), suggesting some degree of mate evaluation. To our knowledge, however, only a few studies have explicitly tested whether amphipod females distinguish between males of different quality. In a choice experiment, female *Megalorchestia californiana* Brandt, 1851 showed no preference for large or small males (Iyengar and Starks 2008). Females also showed less resistance to male advances in the presence of predators, underlining the importance of female behavior in mate choice (Dunn et al. 2008).

Kin Recognition

Incubating females frequently manipulate the embryos in their brood pouch, and during these activities embryos can be lost: females may then retrieve these embryos back into their brood pouch. Embryo retrieval seems to be a common and widespread behavioral mechanism among amphipods, as several examples were reported from distantly related species. For example, females of the assumedly parthenogenetic tube-dweller *Crassicorophium bonellii* (Milne Edwards, 1830)

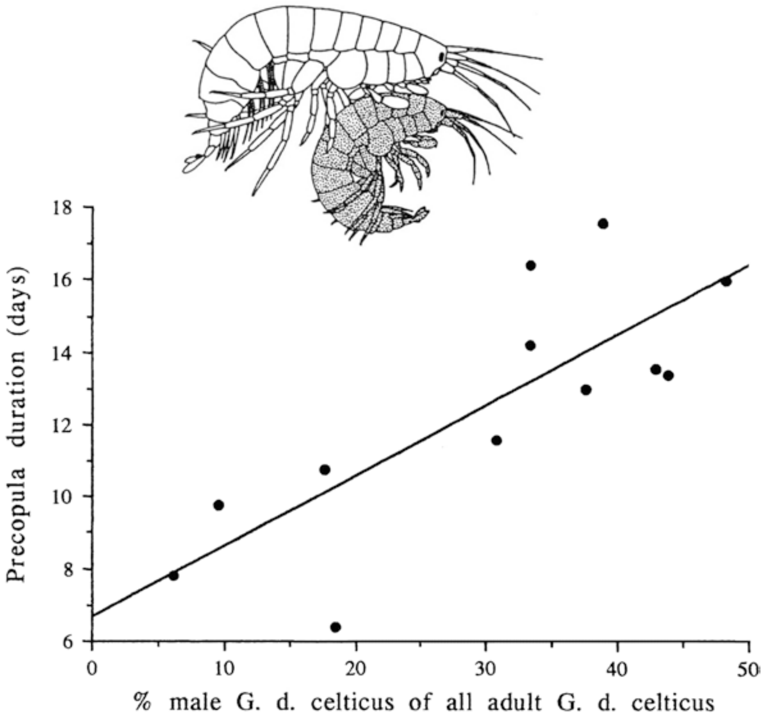


Fig. 6.3 Male *Gammarus duebeni celticus* respond to high male densities with a longer time investment in praecopula (after Dick and Elwood 1996)

replace lost eggs from their marsupium, but do not distinguish between their own brood and embryos from conspecifics (Shillaker and Moore 1987). Moreover, females of the wood-dwelling *Chelura terebrans* Philippi, 1839 collect and retain lost eggs of conspecifics despite their differences in respective developmental stages. As a consequence, the brood pouches of individuals are frequently full of eggs of different developmental stages (Kühne and Becker 1964).

Females of the intertidal *Gammarus palustris* Bousfield, 1969 and its sympatric congener *Gammarus mucronatus* Say, 1818 either eat, ignore, or replace found eggs in their brood pouches (Borowsky 1983). The former species, however, prefers to place eggs in its marsupium if these originated from the same individual or a conspecific. Heterospecific eggs are more likely to get eaten by *G. palustris*, whereas *G. mucronatus* females did not distinguish between the offered egg categories (Borowsky 1983). Although embryo retrieval in general seems to be a common mechanism, there is only one reported example of some degree of true kin discrimination: in *Apherusa jurinei* Milne Edwards, 1830, the degree of embryo replacement depends on the female's reproductive stage (Patterson et al. 2008). Furthermore, the authors showed that females retrieved more of their own embryos than those from conspecifics. In return, foreign embryos engendered a higher level of embryo cannibalism. Female *Crangonyx pseudogracilis* Bousfield, 1958 can also recognize the developmental stage of their embryos and allocate brood care activities accordingly (Dick and Elwood 2006).

A number of amphipod species also engage in extended parental care. Juveniles can cling to, or stay near their mother (Harrison 1940; Lim and Alexander 1986; Aoki and Kikuchi 1991; Thiel 1997; Aoki 1999; Kobayashi et al. 2002) and in some cases the females even cohabit with their growing offspring (Thiel et al. 1997). Females may cohabit for several months with their offspring, as is the case in the burrow-dwelling species *Casco bigelowi* Blake, 1929 (Thiel 1998), but it is not well known whether they can recognize their own offspring or not (Thiel 2007). Not surprisingly, most observations on female-offspring recognition come from species that live above the sediment on mud whips, which they aggressively defend against conspecifics (Mattson and Cedhagen 1989). These authors remarked that small individuals rarely fight when encountering each other on a mud whip, possibly because they are juveniles from the same mother. In contrast, adult individuals, especially if they are from the same sex, regularly fight (Mattson and Cedhagen 1989). However, whether females are able to distinguish their own juveniles from unrelated offspring is unknown. While only a few observations are available for these epibenthic amphipods with extended parental care, even less is known for burrow-dwelling amphipods. Evolution of kin recognition might depend on the probability of encountering unrelated offspring in their burrows: if this is highly unlikely, there might be no need to discriminate kin from non-kin.

Ranking of Conspecifics

Intense male-male competition has evolved into ritualized fighting behavior for mates in some amphipod species which are known to occur in dense populations (e.g. Bowers 1964; Lim and Alexander 1986; Schulz and Alexander 2001). Although direct interference can communicate a male's fitness to competitors, only a few examples of "true" signals which allow for the distinction of higher-ranking versus lower-ranking individuals have been published to date for amphipods.

Males of the talitrid *Megalorchestia californiana* exhibit an enlarged second antenna showing a diagnostic red coloration (Bousfield 1982). Each individual of this semi-terrestrial species digs self-constructed burrows which are only left at night in order to search for food and mates in close vicinity (Bowers 1964). Length and redness intensity of the male antennae are correlated with male body mass (Fig. 6.4a, b). When visible at the burrow's opening, they are most likely to give a visual signal to conspecifics (Iyengar and Starks 2008). In natural populations, the largest males occupy the most attractive locations, being surrounded by the females which expect to profit from a high-quality mate and its resources (Fig. 6.4c; Iyengar and Starks 2008).

Species of the genus *Jassa* inhabit self-constructed tubes (Fig. 6.5a, b) which can be attached adjacent to conspecific tubes in dense aggregations, often forming extensive mats (Fig. 6.5a). After a terminal molt, the males develop thumb-like

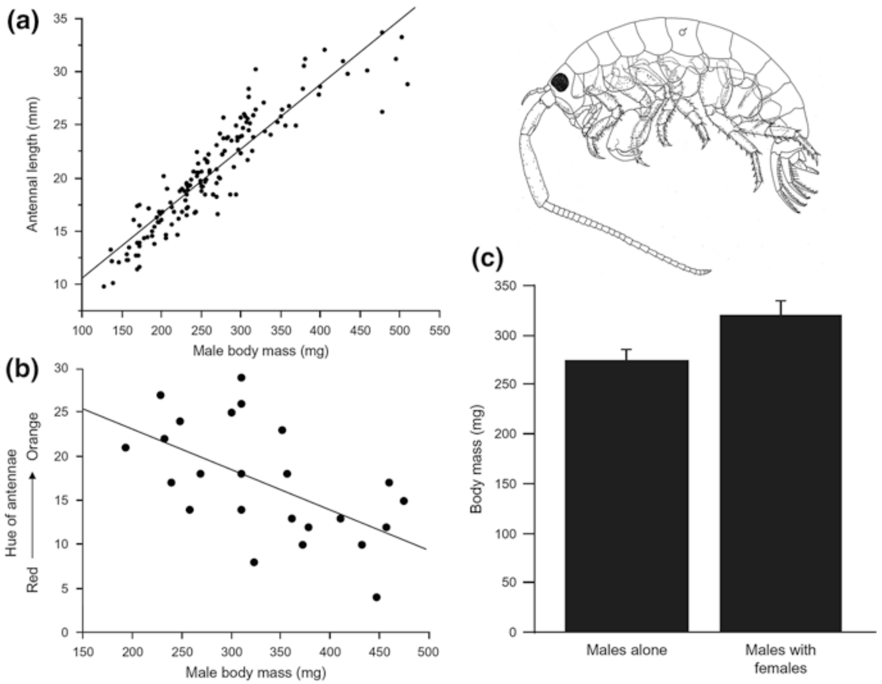


Fig. 6.4 Antennal size and color intensity of male *Megalorchestia californiana* increase with body mass (**a**, **b**), acting as visual signals to conspecifics. As a consequence thereof, large males are more likely to get access to receptive females (**c**), (after Iyengar and Starks 2008; drawing modified after Bousfield 1982)

protuberances on the propodi of the enlarged second gnathopods (Fig. 6.5c), leave their tubes and start roaming in search of receptive females (Fig. 6.5a). Although the thumbs apparently neither play an active role in the course of copulation, nor for fighting off other thumbed males, females are less tolerant to the presence of non-thumbed males (Borowsky 1985a, b; see Sect. Reproductive Quality and Conditions). Conlan (1989) suggested that thumb-size may be a signal to other males, as it is positively correlated with body size. In addition, there is a distinct dimorphism among thumbed *Jassa* males which is determined by food quality in preceding developmental stages: 'Major' males have large body sizes, showing a strongly enlarged antenna 2 and gnathopod 2 with big thumbs; 'minor' males, in contrast, are usually smaller and bear proportionally smaller antennae and gnathopods with smaller thumbs (Conlan 1989, 1990; Clark 1997; Kurdziel and Knowles 2002). These differences in morphology are linked to different mating strategies. Whereas 'major' males guard females by attending their mate's tube opening and fighting off other males, 'minor' males never fight 'majors' but try to evict other 'minors' (Clark 1997). Accordingly, 'minor' form males have to be capable of recognizing a male's rank in order to either avoid them or to fight them off.

In captivity, individuals of *Podocerus* sp. show a surprising behavior in which they form dense masses of individuals with the animals sitting atop of each other

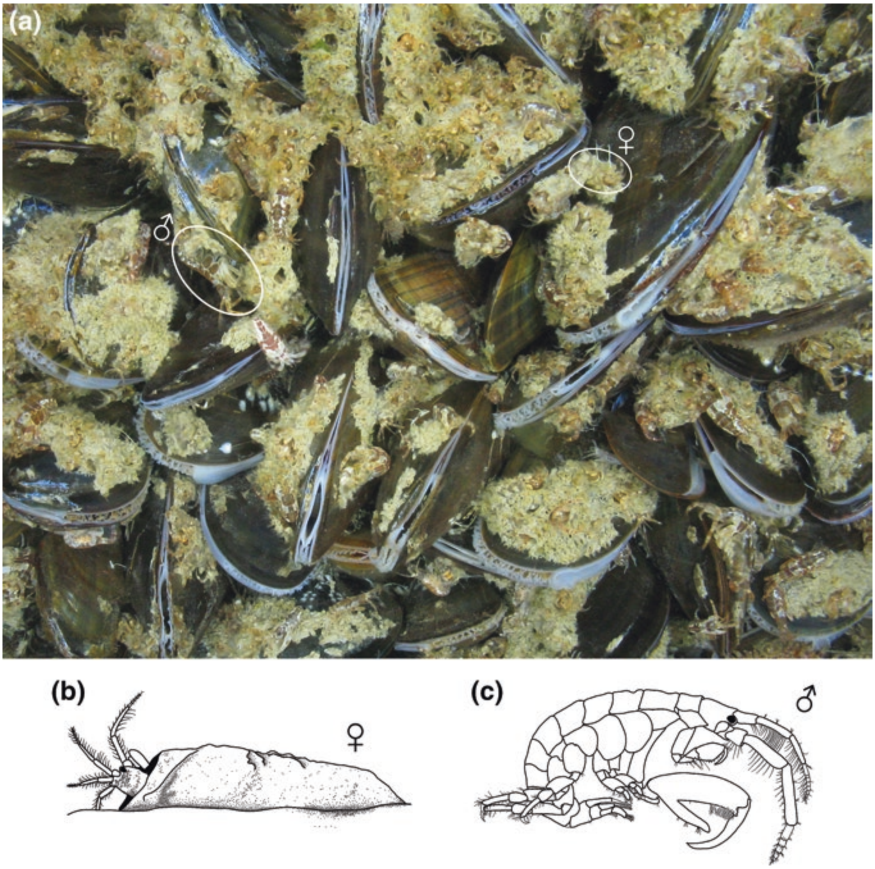


Fig. 6.5 Dense aggregations of *Jassa herdmani* (Walker, 1893) can dominate North Sea fouling communities, partly covering and overgrowing other organisms such as the blue mussel, *Mytilus edulis* Linnaeus, 1758 (**a**; note that beside *Mytilus*, there are only tube-mats in the photograph). Individuals inhabit self-constructed tubes (**b**), which can be attached together in multiple layers. In contrast to the females, large males (**c**) constantly roam around, searching and guarding receptive females [photograph by courtesy of Lars Gutow; drawings modified after Beermann and Purz (2013), and modified and redrawn after a sketch in Dixon and Moore (1997)]

in multiple layers (Barnard et al. 1988). Large individuals seemed to dominate the positions on top, whereas small individuals sit in between larger conspecifics, which could be an indication for a so far unrecognized mechanism of recognition.

No Recognition, Although Expected

Tube-dwelling filter-feeders usually have distinct feeding territories within the ranges of their tube's openings. Even when animal densities are high, direct aggressive interactions among established individuals appear to be rare (Connell 1963;

Dixon and Moore 1997). This could suggest an unrecognized form of social recognition. However, reduction of intraspecific competition seems to be achieved by simple avoidance mechanisms. In addition, positioning of adjacent tubes may be predetermined by preceding aggressive interactions during earlier phases of colonization (Connell 1963; Brawley and Adey 1981; Dixon and Moore 1997).

Conclusion and Outlook

Social recognition in amphipods appears to be largely limited to mate and female-offspring recognition, with some observations that suggest kin recognition within family units in those species where parents and offspring cohabit for extended time periods. To our knowledge, no central-place foraging has been reported for amphipod families and also their potential for fortress defense seems to be very limited. Higher level social recognition, as reported for isopods or crabs (Linsenmair 2007; Diesel and Schubart 2007), may thus be unlikely to have evolved in amphipods. However, the overall lack of research on amphipod behavior impedes firm conclusion as yet.

Nevertheless, there is strong indication for social recognition on various levels in diverse amphipod species, although a lot of this information is anecdotal and little experimental evidence is available. Gregariousness within a species could be a first indication of social interactions, as grouped and isolated individuals may behave differently, or even seek the vicinity of other conspecifics (Campbell and Meadows 1974; Shillaker and Moore 1978; Lobel and Randall 1986). Cooperation between individuals of *Maera loveni* (Bruzelius, 1859) (Atkinson et al. 1982) could even imply the existence of true individual recognition (sensu Gherardi et al. 2012).

The unfortunate lack of detailed information might be due to several reasons, one being the relatively small size of amphipods compared to other common crustacean models such as stomatopods, shrimps, crayfish, lobsters and crabs. However, this size argument should not be an obstacle any longer, as modern optical equipment allows for rigorous and repeatable observations over relatively small scales (see also Ritz et al. 2011). In fact, their small size and direct development can be an advantage, as large populations are easily maintained with relatively few logistic requirements in controlled laboratory environments, even over several generations. Difficulties in species identification, due to close morphological similarities, or due to species with high phenotypic plasticity, might be another reason for limited research on amphipod social behavior: large crabs or shrimps can be identified much easier than tiny amphipods. Another reason for our limited knowledge on amphipod social interactions is the fact that the most promising species live in underground burrows, or in non-transparent tubes, making observations more challenging. We believe that exciting discoveries are lurking behind the tubicolous curtains and below the sediment surface, and we encourage new scholars of crustacean social behavior to overcome the logistic challenges and document the social life of these fascinating creatures.

References

Ahlgren J, Åbjörnsson K, Brönmark C (2011) The influence of predator regime on the behaviour and mortality of a freshwater amphipod, *Gammarus pulex*. Hydrobiologia 671:39–49

Aoki M (1999) Morphological characteristics of young, maternal care behaviour and microhabitat use by caprellid amphipods. J Mar Biol Ass UK 79:629–638

Aoki M, Kikuchi T (1991) Two types of maternal care for juveniles observed in *Caprella monoceros* Mayer, 1890 and *Caprella decipiens* Mayer, 1890 (Amphipoda: Caprellidae). Hydrobiologia 223:229–237

Atkinson RJA, Moore PG, Morgan PJ (1982) The burrows and burrowing behaviour of *Maera loveni* (Crustacea: Amphipoda). J Zool Lond 198:399–416

Aumack CF, Aimsler CD, McClintock JB, Baker BJ (2011) Changes in amphipod densities among macroalgal habitats in day versus night collections along the Western Antarctic Peninsula. Mar Biol 158:1879–1885

Barnard JL, Karaman G (1991) The families and genera of marine gammaridean Amphipoda (except marine gammaroids) Part 1 + 2. Rec Austral Mus 13:866

Barnard JL, Thomas JD, Sandved KB (1988) Behavior of gammaridean Amphipoda: *Corophium*, *Grandidierella*, *Podocerus* and *Gibberosus* (American *Megaluropus*) in Florida. Crustaceana Suppl 13:234–244

Baumgärtner D, Koch U, Rothaupt K-O (2003) Alteration of kairomone-induced antipredator response of the freshwater amphipod *Gammarus roeseli* by habitat. J Chem Ecol 29:1391–1401

Beermann J, Purz AK (2013) Comparison of life history parameters in coexisting species of the genus *Jassa* (Amphipoda, Ischyroceridae). J Crust Biol 33:784–792

Borowsky B (1983) Placement of eggs in their brood pouches by females of the amphipod Crustacea *Gammarus palustris* and *Gammarus mucronatus*. Mar Behav Physiol 9:319–325

Borowsky B (1984) Effects of receptive females' secretions on some male reproductive behaviors in the amphipod crustacean *Microdeutopus gryllotalpa*. Mar Biol 84:183–187

Borowsky B (1985a) Differences in reproductive behavior between two male morphs of the amphipod crustacean *Jassa falcata* Montagu. Physiol Zool 58:497–502

Borowsky B (1985b) Response of the amphipod crustacean *Gammarus palustris* to waterborne secretions of conspecifics and congeners. J Chem Ecol 11:1545–1552

Borowsky B (1991) Patterns of reproduction of some amphipod crustaceans and insights into the nature of their stimuli. In: Bauer RT, Martin JW (eds) Crustacean Sexual Biology. Columbia University Press, New York, pp 33–49

Bowers DE (1964) Natural history of two beach hoppers of the genus *Orchestoidea* (Crustacea: Amphipoda) with reference to their complemental distribution. Ecology 45:677–696

Bousfield EL (1982) The amphipod superfamily Talitroidea in the northeastern Pacific region. I. Familiy Talitridae: systematics and distributional ecology. Pub Biol Ocean 11:80

Brawley SH, Adey WH (1981) The effect of micrograzers on algal community structure in a coral reef microcosm. Mar Biol 61:167–177

Campbell JI, Meadows PS (1974) Gregarious behaviour in a benthic marine amphipod (*Corophium volutator*). Experientia 30:1396–1397

Clark RA (1997) Dimorphic males display alternative reproductive strategies in the marine amphipod *Jassa marmorata* Holmes (Corophioidea: Ischyroceridae). Ethology 103:531–553

Conlan KE (1989) Delayed reproduction and adult dimorphism in males of the amphipod genus *Jassa* (Corophioidea: Ischyroceridae): an explanation for systematic confusion. J Crust Biol 9:601–625

Conlan KE (1990) Revision of the crustacean amphipod genus *Jassa* Leach (Corophioidea: Ischyroceridae). Can J Zool 68:2031–2075

Connell JH (1963) Territorial behavior and dispersion in some marine invertebrates. Res Popul Ecol 5:87–101

Cothran RD, Henderson KA, Schmidenberg D, Relyea RA (2013) Phenotypically similar but ecologically distinct: differences in competitive ability and predation risk among amphipods. Oikos 122:1429–1440

Dick JTA (1992) Simultaneous manipulations of two potential mates by male *Gammarus pulex* (Amphipoda): a mechanism of active mate choice. Crustaceana 62:217–222

Dick JTA, Elwood RW (1989) Assessments and decisions during mate choice in *Gammarus pulex* (Amphipoda). Behaviour 109:235–246

Dick JTA, Elwood RW (1990) Symmetrical assessment of female quality by male *Gammarus pulex* (Amphipoda) during struggles over precopula females. Anim Behav 40:877–883

Dick JTA, Elwood RW (1992) Coexistence and exclusion among *Gammarus* species: behavioural avoidance of interspecific precopulation by male *G. pulex* (Amphipoda). Oikos 64:541–547

Dick JTA, Elwood RW (1996) Effects of natural variation in sex ratio and habitat structure on mate-guarding decisions in amphipods (Crustacea). Behaviour 133:985–996

Dick JTA, Elwood RW (2006) Parent-offspring conflict and motivational control of brooding in an amphipod (Crustacea). Biol Lett 2:501–504

Dick JTA, Elwood RW, Montgomery WI (1995) The behavioural basis of a species replacement: differential aggression and predation between the introduced *Gammarus pulex* and the native *G. duebeni celticus* (Amphipoda). Behav Ecol Sociobiol 37:393–398

Diesel R, Schubart CD (2007) The social breeding system of the Jamaican bromeliad crab *Metopaulias depressus*. In: Duffy JE, Thiel M (eds) Evolutionary ecology of social and sexual systems: crustaceans as model organisms. Oxford University Press, New York, pp 365–386

Dixon IMT, Moore PG (1997) A comparative study on the tubes and feeding behaviour of eight species of corophioid Amphipoda and their bearing on phylogenetic relationships within the Corophioidea. Phil Trans R Soc B 352:93–112

Drolet D, Coffin MRS, Barbeau MA, Hamilton DA (2013) Influence of intra- and interspecific interactions on short-term movement of the amphipod *Corophium volutator* in varying environmental conditions. Estuar Coast 36:940–950

Duarte C, Jaramillo E, Contreras H, Acuña K (2010) Cannibalism and food availability in the talitrid amphipod *Orchestoidea tuberculata*. J Sea Res 64:417–421

Duffy JE (1990) Amphipods on seaweeds: partners or pests? Oecologia 83:267–276

Dunham PJ (1986) Mate guarding in amphipods: a role for brood pouch stimuli. Biol Bull 170:526–531

Dunham PJ, Hurshman AM (1990) Precopulatory mate guarding in the amphipod, *Gammarus lawrencianus:* effects of social stimulation during the post-copulation interval. Anim Behav 39:976–979

Dunham PJ, Alexander T, Hurshman AM (1986) Precopulatory mate guarding in an amphipod, *Gammarus lawrencianus* Bousfield. Anim Behav 34:1680–1686

Dunn AM, Dick JTA, Hatcher MJ (2008) The less amorous *Gammarus*: predation risk affects mating decisions in *Gammarus duebeni* (Amphipoda). Anim Behav 76:1289–1295

Durieux R, Rigaud T, Médoc V (2012) Parasite-induced suppression of aggregation under predation risk in a freshwater amphipod: sociality of infected amphipods. Behav Process 91:207–213

Enright JT (1962) Responses of an amphipod to pressure changes. Comp Biochem Physiol 7:131–145

Galipaud M, Dechaume-Moncharmont F-X, Oughadou A, Bollache L (2011) Does foreplay matter? *Gammarus pulex* females may benefit from long-lasting precopulatory mate guarding. Biol Lett 7:333–335

Gherardi F, Aquiloni L, Tricarico E (2012) Revisiting social recognition systems in invertebrates. Anim Cogn 15:745–762

Gunnill FC (1984) Differing distributions of potentially competing amphipods, copepods and gastropods among specimens of the intertidal alga *Pelvetia fastigiata*. Mar Biol 82:277–291

Hallberg E, Skog M (2011) Chemosensory sensilla in crustaceans. In: Breithaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, New York, pp 103–121

Harrison RJ (1940) On the biology of the Caprellidae. Growth and moulting of *Pseudoprotella phasma* Montagu. J Mar Biol Ass UK 24:483–493

Iribarne O, Fernandez M, Armstrong D (1995) Precopulatory guarding-time of the male amphipod *Eogammarus oclairi*: effect of population structure. Mar Biol 124:219–223

Iyengar VK, Starks BD (2008) Sexual selection in harems: male competition plays a larger role than female choice in an amphipod. Behav Ecol 19:642–649

Kinne O (1953) Zur Biologie und Physiologie von *Gammarus duebeni* Lillj., II: Über die Häutungsfrequenz, ihre Abhängigkeit von Temperatur und Salzgehalt, sowie über ihr Verhalten bei isoliert gehaltenen und amputierten Versuchstieren. Zool Jahrb 64:183–206

Kinne O (1960) *Gammarus salinus*—Einige Daten über den Umwelteinfluss auf Wachstum, Häutungsfolge, Herzfrequenz und Eientwicklungsdauer. Crustaceana 1:208–218

Kobayashi T, Wada S, Mukai H (2002) Extended maternal care observed in *Pallorchestes ochotensis* (Amphipoda, Gammaridea, Tallitroidea, Hyalidae). J Crust Biol 22:135–142

Kolding S (1986) Interspecific competition for mates and habitat selection in five species of *Gammarus* (Amphipoda: Crustacea). Mar Biol 91:491–495

Krång AS, Baden SP (2004) The ability of the amphipod *Corophium volutator* (Pallas) to follow chemical signals from con-specifics. J Exp Mar Biol Ecol 310:195–206

Krapp-Schickel T (2013) New or amended data on Mediterranean Amphipoda: genera *Dexamine*, *Ericthonius* and *Stenothoe*. Zootaxa 3613:125–145

Kühne H, Becker G (1964) Der Holz-Flohkrebs *Chelura terebrans* Philippi (Amphipoda, Cheluridae) Morphologie, Verbreitung, Lebensweise, Verhalten, Entwicklung und Umweltabhängigkeit. Beihefte Z Angew Zool 1:3–141

Kullmann H, Thünken T, Baldauf SA, Bakker TCM, Frommen JG (2008) Fish odour triggers conspecific attraction behaviour in an aquatic invertebrate. Biol Lett 4:458–460

Kurdziel JP, Knowles LL (2002) The mechanisms of morph determination in the amphipod *Jassa*: implications for the evolution of alternative male phenotypes. Proc R Soc B 269:1749–1754

Lewis SE, Dick JTA, Lagerstrom K, Clarke HC (2010) Avoidance of filial cannibalism in the amphipod *Gammarus pulex*. Ethology 116:138–146

Lim STA, Alexander CG (1986) Reproductive behaviour of the caprellid amphipod, *Caprella scaura typica*, Mayer 1890. Mar Behav Physiol 12:217–230

Linsenmair KE (2007) Sociobiology of terrestrial isopods. In: Duffy JE, Thiel M (eds) Evolutionary ecology of social and sexual systems: crustaceans as model organisms. Oxford University Press, New York, pp 339–364

Lobel PS, Randall JE (1986) Swarming behavior of the hyperiid amphipod *Achnylomera blossevilli*. J Plankton Res 8:253–262

MacNeil C, Dick JTA, Elwood R (1997) The trophic ecology of freshwater *Gammarus* spp. (Crustacea: Amphipoda): problems and perspectives concerning the Functional Feeding Group concept. Biol Rev 72:349–364

MacNeil C, Dick JTA, Elwood R (1999) The dynamics of predation on *Gammarus* spp. (Crustacea: Amphipoda). Biol Rev 74:375–395

Mattson S, Cedhagen T (1989) Aspects of the behaviour and ecology of *Dyopedos monacanthus* (Metzger) and *D. porrectus* Bate, with comparative notes on *Dulichia tuberculata* Boeck (Crustacea: Amphipoda: Podoceridae). J Exp Mar Biol Ecol 127:253–272

McDonald PS, Bingham BL (2010) Comparing macroalgal food and habitat choice in sympatric, tube-building amphipods, *Ampithoe lacertosa* and *Peramphithoe humeralis*. Mar Biol 157:1513–1524

Moore PG (1994) Observations on the behaviour of the scavenging lysianassoid *Orchomene zschaui* (Crustacea: Amphipoda) from South Georgia (South Atlantic). Mar Ecol Prog Ser 113:29–38

Moore PG, Wong YM (1995) *Orchomene nanus* (Krøyer) (Amphipoda: Lysianassoidea), a selective scavenger of dead crabs: feeding preferences in the field. J Exp Mar Biol Ecol 192:35–45

Myers AA (2009) Photidae. In: Lowry JK, Myers AA (eds) Benthic Amphipoda (Crustacea: Peracarida) of the Great Barrier Reef, Australia. Zootaxa 2260:771–799

Myers AA, McGrath D (1984) A revision of the North-East Atlantic species of *Ericthonius* (Crustacea: Amphipoda). J Mar Biol Ass UK 64:379–400

Patterson L, Dick JTA, Elwood RW (2008) Embryo retrieval and kin recognition in an amphipod (Crustacea). Anim Behav 76:717–722

Platvoet D, Song Y, Li S, Van Der Velde G (2007) Description of the lateral line organ of *Dikerogammarus villosus* (Sowinsky, 1984), with discussion on its function (Peracarida, Amphipoda). Crustaceana 80:1373–1392

Poulton MJ, Thompson DJ (1987) The effects of the acanthocephalan parasite *Pomphorhynchus laevis* on mate choice in *Gammarus pulex*. Anim Behav 35:1577–1579

Premke K, Klages M, Arntz WE (2006) Aggregations of Arctic deep-sea scavengers at large food falls: temporal distribution, consumption rates and population structure. Mar Ecol Prog Ser 325:121–135

Premke K, Muyakshin S, Klages M, Wegner J (2003) Evidence for long-range chemoreceptive tracking of food odour in deep-sea scavengers by scanning sonar data. J Exp Mar Biol Ecol 285–286:283–294

Rigolet C, Dubois SF, Droual G, Caisey X, Thiébaut E (2012) Life history and secondary production of the amphipod *Haploops nirae* (Kaim-Malka, 1976) in the Bay of Concarneau (South Brittany). Estuar Coast Shelf Sci 113:259–271

Ritz DA, Hobday AJ, Montgomery JC, Ward AJW (2011) Social aggregation in the pelagic zone with special reference to fish and invertebrates. Adv Mar Biol 60:161–227

Sainte-Marie B (1992) Foraging of scavenging deep-sea lysianassoid amphipods. In: Rowe GT, Pariente V (eds) Deep-sea food chains and the global carbon cycle. Kluwer Academic Publishers, Dordrecht, pp 105–124

Schulz MK, Alexander CG (2001) Aggressive behaviour of *Caprella scaura typica* Mayer, 1890. (Crustacea: Amphipoda). Mar Fresh Behav Physiol 34:181–187

Sheader M, Van Dover CL, Shank TM (2000) Structure and function of *Halice hesmonectes* (Amphipoda: Pardaliscidae) swarms from hydrothermal vents in the eastern Pacific. Mar Biol 136:901–911

Shillaker RO, Moore PG (1978) Tube building by the amphipods *Lembos websteri* Bate and *Corophium bonnellii* Milne Edwards. J Exp Mar Biol Ecol 33:169–185

Shillaker RO, Moore PG (1987) The biology of brooding in the amphipds *Lembos websteri* Bate and *Corophium bonnellii* Milne Edwards. J Exp Mar Biol Ecol 110:113–132

Thiel M (1997) Another caprellid amphipod with extended parental care: *Aeginia longicornis*. J Crust Biol 17:275–278

Thiel M (1998) Reproductive biology of a deposit-feeding amphipod, *Casco bigelowi*, with extended parental care. Mar Biol 132:107–116

Thiel M (2007) Social behavior of parent–offspring groups in crustaceans. In: Duffy JE, Thiel M (eds) Evolutionary ecology of social and sexual systems: crustaceans as model organisms. Oxford University Press, New York, pp 294–318

Thiel M (2011a) Chemical communication in peracarid crustaceans. In: Breithaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, New York, pp 199–218

Thiel M (2011b) The evolution of sociality: peracarid crustaceans as model organisms. In: Asakura A (ed) New frontiers in crustacean biology—proceedings of the TCS summer meeting, Tokyo, 20–24 Sept 2009. Brill Academic Publishers, Leiden, pp 285–297

Thiel M, Sampson S, Watling L (1997) Extended parental care in two endobenthic amphipods. J Nat Hist 31:713–725

Thomas F, Renaud F, Cezilly F (1996) Assortative pairing by parasitic prevalence in *Gammarus insensibilis* (Amphipoda): patterns and processes. Anim Behav 52:683–690

Thurston MH (1979) Scavenging abyssal amphipods from the North-East Atlantic Ocean. Mar Biol 51:55–68

Väinölä R, Witt JDS, Grabowski M, Bradbury JH, Jazdzewski K, Sket B (2008) Global diversity of amphipods (Amphipoda; Crustacea) in freshwater. Hydrobiologia 595:241–255

Van Tomme J, Van Colen C, Degraer S, Vincx M (2012) Encounter competition partly explains the segregation of the sandy beach amphipods *Bathyporeia pilosa* and *Bathyporeia sarsi*. A mesocosm experiment. J Exp Mar Biol Ecol 438:118–124

Vitaliano J, Packer D, Reid R, Guida V (2013) Broad-scale, dense amphipod tube aggregations on the sea bed: implications for resource species that utilize benthic habitats. Fish Oceanogr 22:61–67

Wenngren J, Ólafson E (2002) Intraspecific competition for food within and between year classes in the deposit-feeding amphipod *Monoporeia affinis*—the cause of population fluctuations? Mar Ecol Prog Ser 240:205–213

Wisenden BD, Pohlman SG, Watkin EE (2001) Avoidance of conspecific injury-released chemical cues by free-ranging *Gammarus lacustris* (Crustacea: Amphipoda). J Chem Ecol 27:1249–1258

Wyatt TD (2011) Pheromones and behavior. In: Breithaupt T, Thiel M (eds) Chemical communication in crustaceans. Springer, New York, pp 23–38

Chapter 7
Social Recognition in the Arachnida

André Walter and Trine Bilde

Abstract More than 99 % of arachnid species are solitary, aggressive and often cannibalistic predators. A few species are social and cooperative, but they do not reach the level of eusociality found in some insects. Kin recognition is suggested to be a key feature for the evolution of cooperation and sociality and thus found predominantly in those few species. While kin recognition and social interactions are well investigated in spiders, these behaviours are understudied in other arachnid taxa. Nevertheless, social species are also known in the Acari, Pseudoscorpiones, Scorpiones, Opiliones and Amblypygi. Still, we have limited information on the adaptive value of social recognition in arachnids, how it is facilitated and maintained. While this field of research is still young, it has produced some encouraging results. This chapter reviews the knowns and the unknowns of social recognition mechanisms with respect to their importance for the evolution of arachnid sociality. We will particularly focus on kin recognition and kin discrimination. First, we shortly introduce the evolution of sociality in arachnids which provides the background for the understanding of the different recognition and discrimination mechanisms explained subsequently. Further, we illustrate the interspecific discrimination abilities of arachnids, and present the state of the art on intraspecific recognition and kin recognition in spiders and other arachnids. This chapter illustrates that various social recognition abilities and especially kin recognition exist in social but also non-social arachnids. These mechanisms allow different species to distinguish between familiar and foreign, or related and unrelated individuals, to either support or discriminate against them. In contrast to eusocial insects, the necessity of maintaining kin recognition abilities often appears to be obscure and highly context-dependent. Thus, a generalisation of its adaptive value in arachnids is not possible. There is some evidence for the concept of kin recognition facilitating the evolutionary transition from subsocial

---

A. Walter (✉) · T. Bilde
Department of Bioscience, Genetics, Ecology and Evolution,
Aarhus University, Ny Munkegade 116, 8000 Aarhus C, Denmark
e-mail: andre.walter@bios.au.dk

L. Aquiloni and E. Tricarico (eds.), *Social Recognition in Invertebrates*,
DOI 10.1007/978-3-319-17599-7_7

to permanently social living. However, kin recognition has not yet been demonstrated in permanently social species and is thus subject of ongoing research. It might have been lost during evolution due to the lack of encounters with unrelated individuals in permanent arachnid societies or replaced by direct benefits of cooperation. Finally, we discuss some research gaps and new approaches to improve the knowledge of the adaptive significance of kin recognition in arachnids.

Social Recognition in the Arachnida

Most arachnid species are solitary, aggressive and sometimes cannibalistic. Compared to insects, group living in these arthropods is an exception. More than 99 % of all species are solitary (Rayor and Taylor 2006). The level of sociality too, does not reach that of eusocial insects (Plateaux-Quènu and Roland 1997). Based on the less pronounced behavioural division of labour and the lack of a caste system, Whitehouse and Lubin (2005) refer to arachnid sociality as the ‘poor cousin of insect sociality’. Within the Arachnida, social interactions are well investigated in the Araneae but understudied in other taxa. Apart from spiders, social species are known in the Acari, Pseudoscorpiones, Scorpiones, Opiliones and Amblypygi. Some of the smaller groups, like Palpigradi and Ricinulei are very poorly known and thus a more general understanding of social aspects is not yet available (Rayor and Taylor 2006). Social recognition is a broad term that includes species recognition, and recognition of mating partners. As an example, courtship behaviour, which is extremely elaborate in many arachnids, has been suggested to function to identify species in a mate choice context and might therefore be considered a form of social recognition. In this chapter, we focus on the function of recognition in a social context including lose aggregations, group formations and cooperative behaviours. Our review on the social recognition abilities of arachnids will mainly focus on their impact on the evolution of group living and cooperation in this arthropod group.

For the evolution of cooperation and sociality, especially kin recognition is suggested to be a key feature (Hamilton 1964; Boomsma 2007), as documented in cooperatively breeding birds and mammals as well as the social insects (Griffin and West 2003). So far, we have still little information on whether arachnids show kin recognition, how kin recognition is facilitated, and the role of kin discrimination in social interactions. This chapter will review the state of the art of social recognition abilities in arachnids with a special focus on kin recognition, and we will thus start with a brief review of the evolution of sociality in these arthropods. In insects, sociality and social recognition have been extensively investigated and are discussed in this book. In particular, the importance and underlying mechanisms of kin recognition are well understood in insects, but their occurrence in arachnids is both astonishing and sometimes confusing, and the adaptive significance is often ambiguous. To date this field of research is still young and yet has produced some encouraging insights.

Sociality in Arachnids

Although rare in arachnids, group formation can be beneficial under certain conditions. It may help to reduce the risk of predation (e.g. Henschel 1998), increase foraging efficiency (e.g. Ward 1986) and increase the chance of finding a mating partner (e.g. Johannesen et al. 2007). As arachnids are predominantly predators, foraging motivation is considered to be a significant driving force that explains the advantage of group living in these animals (Fig. 7.1) (Brach 1975; Nentwig 1985; Wickler and Seibt 1993; Majer et al. 2013a). In groups, arachnids are able to better monopolise locally rich food sources; and larger prey animals or a greater number of items may be better overwhelmed when attacked communally. The size of prey can be between four times larger in some Pseudoscorpions (Tizo-Pedroso and Del-Claro 2007) to 16 times larger in some spiders (Ward 1986) compared to the weight of a single individual. Powers and Avilés (2007) found that the average size of prey items rather than the amount of prey biomass positively correlates with the level of sociality in *Anelosimus* spiders. Such coherency may be particularly important for juveniles as the group foraging mode increases survival and facilitates a reasonably quick development. Food availability is likely to facilitate group cohesion and tolerance to other individuals in close proximity. The richer a food source, the stronger is the bonding of groups mediated by intraspecific tolerance (Gundermann et al. 1993; Schneider 1995; Kim 2000). In contrast, under low food conditions, competition over prey (Bilde et al. 2007) or increased cannibalism (Bilde and Lubin 2001) may counteract group living. Consequently, cooperation has been found in environments with temporally stable prey abundances such as the tropics (Yip et al. 2008; Del-Claro and Tizo-Pedroso 2009; Majer et al. 2013b). On the other hand, lower prey availability or greater prey size may render cooperation more necessary.

The pathways of group formation in arachnids have been intensively investigated in spiders, and the evolutionary concepts have often been adopted for other taxa. One of the most important prerequisites for social bonding is tolerance of other individuals. As predators, arachnids usually behave aggressively not only towards potential prey but also towards conspecifics that may represent competitors as well as potential prey. However, many species of spiders, scorpions and pseudoscorpions exhibit maternal care, and the brood remain in close proximity to the mother. Accordingly, the juveniles show lower intraspecific aggression levels. Overcoming aggression or extending juvenile tolerance respectively, is crucial for moving on to the next stage, interaction (Kullmann 1968), which facilitates the formation of groups. So, intraspecific tolerance allows the development of gregarity as one of the simplest forms of social interactions. Loose short-term aggregations to share a shelter, to exploit a resource or to protect themselves against predators are known for several arachnids, such as harvestmen (Chelini et al. 2012), scorpions (Polis and Lourenço 1986), mites (Mailleux et al. 2011) and spiders (Buskirk 1981). The most advanced level of social living is cooperation, characterised by individuals working together to accomplish a certain task to obtain individual fitness benefits (Whitehouse and Lubin 2005). Group tasks may comprise the collective construction of retreats, brood chambers and capture webs (in spiders), prey capture, communal feeding and brood care

Fig. 7.1 A group of six *Stegodyphus dumicola* females attacking grasshopper caught in the capture web of the colony. (*photo* André Walter)

(Kullmann 1972; Lubin and Bilde 2007). However, even the most advanced social species still do not reach the eusocial level of insects with strict worker castes and complex social coordination (Lubin and Bilde 2007), although recent studies indicate the presence of basic forms of division of labour at least in some social arachnids (Grinsted et al. 2013; Settepani et al. 2013; Wright et al. 2014).

Generally, the type and organization of social interactions differ among group living arachnid species. The presence or absence of cooperation among group members, and the duration of the social and cooperative stage, is crucial for the distinction of different types of sociality. Species with close-together living but typically without cooperation and allo-maternal care are ‘gregarious’ or ‘colonial’, and also some ‘kleptoparasitic’ species fall into this category that we refer to as ‘colonial’ (Agnarsson 2002; Bilde and Lubin 2011). Their group formation is the result of aggregations of mainly unrelated individuals, often around a rich food source, but they remain solitary in their behaviour and do not cooperate with conspecifics (Uetz and Hieber 1997). Individuals of ‘subsocial’ and ‘social’ species show cooperation, and groups originate from family bonding. While subsocial species form groups only periodically, the social species live in permanent colonies (Lubin and Bilde 2007; Bilde and Lubin 2011). In the subsocial state, offspring of a single mother form groups to cooperate temporarily, but dispersal occurs before mating and most species adopt solitary living. Periodic social living is facilitated by the extended maternal care, hence the term subsocial behaviour. Social species build permanent nests, sometimes with overlapping generations, and show reproductive skew and allo-maternal care. They can be compared with cooperative breeders (like in birds and mammals) that have helpers at the nest that help rearing the offspring.

Evolution of Sociality in Arachnids

The evolutionary progression to sociality proposes two major scenarios that are generally accepted to explain the appearance of group living in Arachnids, the ‘parasocial route’ and the ‘subsocial route’ (Avilés 1997; Plateaux-Quènu et al. 1997; Schneider 2002). Both scenarios have led to different degrees of sociality reaching from colonial, over subsocial to permanent cooperative species (Whitehouse and Lubin 2005; Lubin and Bilde 2007).

The ‘parasocial route’ describes the evolution of group living via aggregation of individuals of otherwise solitarily living species (Wickler and Seibt 1993). In colonial spiders, for example, colonies of webs can be found clustered around a rich food source in order to exploit it more efficiently. The spiders use common frame threads, but each individual maintains its own webs and feeds solitarily, and conspecifics may not be accepted within individual webs (Jackson 1982; Bowden and Jackson 1988). Aggregations are associated with close contact among individuals. Thus, this scenario requires the overcoming of intraspecific aggression and the abandonment of territoriality. In many harvestmen, pseudoscorpions and scorpions individuals temporarily aggregate and tolerate each other to seek shelter or to exploit a rich resource in a spatially limited habitat, but show no indication of cooperation (Rayor and Taylor 2006), which is the key feature of permanently social living. The ‘parasocial route’ may also explain the evolution of kleptoparasitism, where, for example, spider species aggregate in webs of their hosts to feed on prey remains (Agnarsson 2002). However, the ‘parasocial route’ is also associated with the risk of aggressions as a result of competition around a food source, and is therefore unlikely to explain the occurrence of cooperative sociality in arachnids.

The ‘subsocial route’ pathway describes the evolution of sociality via extended maternal care. Here, related offspring stay together over a period of time after hatching and display intra-group tolerance. Ultimately, permanent sociality is achieved by the complete elimination of pre-mating dispersal. Maternal care is widespread amongst arachnids (Yip and Rayor 2014) and it seems likely that extended maternal care and the resulting formation of family sibling groups is a pre-condition for sociality to evolve (Lubin and Bilde 2007). For the maintenance of group cohesion, juvenile dispersal has to be delayed to prolong the time of intraspecific interaction, mainly between mother and offspring, to allow selection to act on behaviours that facilitate further social evolution. In many arachnid species the mother individual cares for the young by protecting them against predators, building a sheltering nest, by providing them with captured prey, by feeding them through regurgitation of nutritious fluids or by scarifying herself to the offspring to maximize maternal investment (Lubin and Bilde 2007; Del-Claro and Tizo-Pedroso 2009). If juveniles stay together for several instars to cooperate beyond the mother's death, the criterion of a subsocial relation is fulfilled (cf. definition in Agnarsson et al. 2006). In an even narrower sense, extended maternal care might be already considered as a subsocial behaviour. However, at the same time the pre-mating dispersal drive of the young also needs to be suppressed to ensure group cohesion over a certain time (Gundermann et al. 1993; Schneider 1995; Avilés 1997). Usually, juveniles live together until competition for food triggers dispersal, or until they have reached a species-specific body mass or size to disperse. Wickler and Seibt (1993) suggested a more specific term for the 'subsocial route', referring to a 'sibling route' in the evolution of sociality. The evolution of permanent sociality through cooperation among siblings would be favoured by inclusive fitness benefits and thus kin selection (Hamilton 1964; Maynard Smith 1964). Especially in a transitional stage and if individuals encounter conspecifics of varying relatedness, this requires recognition mechanisms to direct cooperative actions towards kin.

Interspecific Discrimination in Arachnids

Arachnid species that show social behaviour are characterised by high intra- and often interspecific tolerance when forming groups (spiders: Seibt and Wickler 1987/scorpions: Shivashankar 1994; Lourenço and Cloudsley-Thompson 2011/pseudoscorpions: Weygoldt 1969; Del-Claro and Tizo-Pedroso 2009/harvestmen: Machado and Macías-Ordoñez 2007; Chelini et al. 2012/mites, Mori and Saito 2006; Mailleux et al. 2011; Strodl and Schausberger 2012b). Unless there is indiscriminate tolerance of any foreign individual, these species must have developed recognition abilities to discriminate acceptable group members from those that will be refused. Given ageneral advantage of group living, species may choose to associate with congeners, unrelated conspecifics or only with siblings. The latter is of particular interest in subsocial and social arachnids.

The most basic level of recognition is that of dead and alive. Brach (1977) found in the social spider *Anelosimus studiosus* (Theridiidae) that any conspecific individual that has joined the colony is considered as co-operator as long as it is alive. Dead spiders will be treated as prey, an action that of course may also be considered as sanitation behaviour to keep the communal nest healthy. The distinction on the next higher level refers to the genus or species level. Individuals that intrude into a colony but belong to a completely different taxon may potentially represent predators or kleptoparasites. In *Stegodyphus sarasinorum* (Erisidae), Kullmann (1972) noticed an interesting recognition mechanism in which individuals of the species recognise erisid-typical (spider family Erisidae) body features but without having the ability to discriminate between different species or conspecifics. Consequently, Kullmann (1972) showed in manipulative experiments that an association between different species is possible through a reduced interspecific aggression level. The recognition mechanism has been suggested to be based on chemosensitive perception via pheromones (Kullmann 1972). A similar congeneric acceptance has also been revealed for two social *Stegodyphus* species (Seibt and Wickler 1988). The interspecific acceptance is high enough to even allow the formation of mixed species groups that perfectly cooperate. Experimentally brought together in the lab, *Stegodyphus mimosarum* (Fig. 7.2) and *Stegodyphus dumicola* cooperatively build webs and forage (Seibt and Wickler 1988). Later Grinsted et al. (2012) found a similar behaviour realised in the wild. Two *Chikunia* species (Araneae; Theridiidae) were found to form mixed colonies. These spiders do not forage together, but lab experiments suggest that there might be interspecific brood care as females of one species adopt the young of the other (Grinsted et al. 2012). Other examples on congeneric group member acceptance can be found in social and subsocial species of the theridiid spider genus *Anelosimus* (Samuk and Avilés 2013), or in gregarious species of the harvestmen genus *Serracutisoma* (Chelini et al. 2012). However, in the latter example individuals show a clear preference to associate with conspecifics indicating that species discrimination is also present.

The fact that many group living species tolerate congeners may indicate that the evolution of social interactions via the para-social route has started with a general lowering of aggression to gain direct benefits of association. However, permanent sociality and cooperation in arachnids appear to only evolve through the sub-social route based on kin selected benefits (Anthony 2003; Lubin and Bilde 2007). Hence, tolerance alone is not a mean of inter- and intra-specific cooperation. Tolerance towards conspecifics and low interspecific aggression may, however, play a significant role in the evolution of kleptoparasitism. Agnarsson (2002) noted that these behavioural patterns can be found in kleptoparasitic *Argyrodes*—species (Theridiidae). In social species, the tolerance is mutual between juveniles and the larger mother individual. Usually, a larger animal might be considered as a predator. Therefore, not trying to escape when being in its close proximity is not self-evident. Small *Argyrodes* spiders of different species had to overcome this barrier to enter the host spider's web that is always much larger in body size (Agnarsson 2002). As more than one *Argyrodes* individual and sometimes more species occupy a host web, additional intraspecific tolerance is essential to avoid competitive fights that may alert the host spider. Hence, it is reasonable to assume that at least in the family Theridiidae, which comprises social and as well as kleptoparasitic species, the same tolerance-mechanisms may represent the evolutionary origin for both lifestyles.

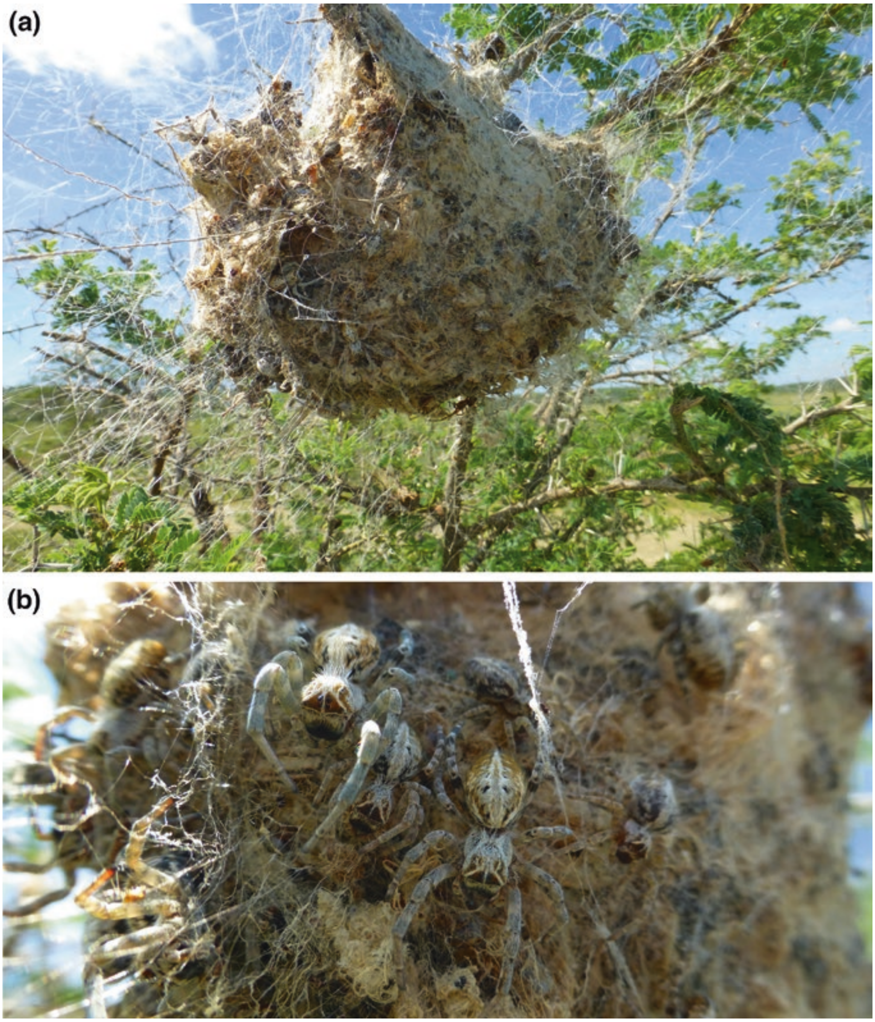


Fig. 7.2 A nest of social *Stegodyphus dumicola* spiders (Erisidae) in Weenen Nature Reserve/South Africa. **a** total view, **b** close up. (*Photos* André Walter)

The cues used to identify members of the same species are various and not always fully understood. Both tactile (Wilson 1971; Brach 1975) and chemical stimuli (Kullmann 1972) have been described as effective discrimination cues used in different species. In particular, pheromones play an important role for arachnid species recognition but also for intraspecific attraction to form groups (spiders: Seibt and Wickler 1988; Evans and Main 1993; Trabalon and Assi-Bessékon 2008/whip spiders: Hebets and Chapman 2000; Walsh and Rayor 2008/mites: Sato et al. 2003; Mailleux et al. 2011; Clotuche et al. 2012). In some social spider species, pheromones deposited on silk will attract individuals to form a group or to join an already established one (*Diaea socialis*, Evans and Main 1993; *S. mimosarum* and *S. dumicola*, Seibt and Wickler 1988). Chemical cues may also be used by particular conspecifics in specific contexts or functions. Females of *D. socialis* are not attracted to juvenile silk (Evans and Main 1993), and the silk of incubating females of the subsocial *Coelotes terrestris* (Agelenidae) attracts mated females but repels virgins (Trabalon and Assi-Bessekon 2008).

It may not surprise that species recognition is widespread also among arachnids as it is an important mechanism to ensure intraspecific matings. Its role for composing groups with conspecifics only is nevertheless still understudied. Species recognition may facilitate the evolution of cooperation through behavioural similarities among individuals of the same species. The nature of interactions among conspecifics may depend on familiarity, developmental stage, sex, and, as shown later, relatedness. For example, in the predaceous mite *Phytoseiulus persimilis* larvae stay together in groups until they moult into protonymphs. These larvae show a preference for grouping with individuals that they are familiar with because they were previously exposed to the same environment, whereas other factors like kinship do not significantly influence aggregation behaviour (Strodl and Schausberger 2012a). Yet another form of discrimination based on sex can be found in the social theridiid spider *A. studiosus*. Conspecific intruders are accepted in the colony, but this does not account for the scenario of a resident adult female encountering another immigrant adult female (Brach 1977). The resulting fight can be considered as competition over a nest and foraging site that is chosen by the resident female to raise her own offspring. The developmental stage may additionally be an important factor to trigger either aggression or cooperative behaviour (e.g. Yip et al. 2012). It is possible that intruding subadult individuals benefit the colony for example by increasing the probability of survival, whereas adult conspecific females are detrimental through the increased competition between offspring of the two families.

In *S. mimosarum* and *S. dumicola* the mother will sooner or later be eaten by her young spiderlings ('matriphagy'). These spiders are semelparous and although not unambiguously proven yet, it is likely that mothers signal to the young to consume her at a certain point in time after regurgitation feeding has started. However, at this stage juvenile spiders not only eat their mother but would also attack any other female of their mother's age (thus also called 'gerontophagy' by Seibt and Wickler 1987). In the subsocial spider *Stegodyphus lineatus* the mother feeds her young after hatching but also provides food to unrelated conspecific young. She only does this, however, if they are within the same instar as her own offspring (Schneider 2002). This maternal behaviour suggests that physiological stage and not discrimination per se is involved in this extreme form of maternal care. Nursing females of the subsocial agelenid spider *C. terrestris* are tolerant to related and unrelated juvenile individuals, but when experimentally confronted with young in the pre-laying or incubating state they would occasionally attack them (Assi-Bessékon and Horel 1996). Cuticular chemical cues have been suggested to mediate this discrimination mechanism (Assi-Bessékon 1997).

With permanent sociality where colonies persist over several years, some species show complete overlapping of generations (e.g. *Anelosimus*) whereas others show partial overlap (e.g. *Stegodyphus*). Permanent social group formation is not only favoured by higher protection and efficiency of foraging, but also by indirect fitness benefits mediated by reproductive skew and allo-maternal brood care that increase survival and reproduction at the colony level (Grinsted and Bilde 2013). When it comes to reproduction, inclusive fitness theory (Hamilton 1964) predicts that cooperative breeding should evolve among related individuals. Intraspecifically, further discrimination mechanisms may be necessary to optimise this level of cooperation. If cooperation evolves from family groups, kin recognition and kin discrimination may not evolve, simply because interactions among non-kin are rare. In this case, either 'familiarity' by recognition of nest mates, or a simple rule stating 'cooperate with nest mates' will effectively have the same evolutionary outcome as kin-mediated interactions (Griffin and West 2003; Schneider and Bilde 2008).

Intraspecific Discrimination and Kin Recognition

Kin recognition describes mechanisms that may lead to differential treatment of conspecifics based on genetic relatedness (Sherman et al. 1997). Following kin selection theory, kin directed cooperation is favoured by inclusive fitness benefits, i.e. the sum of own direct fitness and indirect fitness of relatives with whom they share genes identical by descent (Hamilton 1964; Maynard Smith 1964). Cooperation is expected to evolve when individuals gain higher inclusive fitness by helping to raise offspring of close relatives than they would through own reproduction. This coherency also known as 'Hamilton's rule' applies for many social insect systems as well as cooperatively breeding vertebrates (Boomsma 2007; Griffin and West 2003). It follows that mechanisms that allow recognising kin and directing help towards them will be favoured by selection. Kin recognition has been documented in a number of subsocial arachnids (see below) and appears to play a role in the evolution of cooperation. Kin recognition may also be important in solitary arachnids that are prone to early life competition or cannibalism, as it occurs in some predatory mites (Schausberger 2007; Strodl and Schausberger 2012a, b). As many taxonomic groups have not been studied (Table 7.1), general conclusions about the occurrence and adaptive significance of kin recognition cannot be drawn. However, based on the present data its benefits seem to be unequally distributed across the taxon and often not easy to reveal (Evans 1999). It is important to note that the apparent lack of kin discrimination does not necessarily imply that this trait is absent; it may simply not be in use in relation to the behaviours under investigation. Likewise, the ability to recognise kin does not necessarily imply that nepotism through kin-directed helping takes place (cf. Waldman et al. 1988). For example, in subsocial *Stegodyphus* spiders kin recognition mechanisms have been found (see below) but behavioural differentiations between related and unrelated individuals are not always noticeable (Schneider 1996). Finally, it is important to distinguish between genetic kin discrimination and familiarity, where discrimination is based upon recognition of individuals and not their genetic relatedness. While the evolutionary outcome of these two modes of recognition could be the same, they represent fundamentally different mechanisms of recognition (Schneider and Bilde 2008). Some studies putatively reveal kin discrimination although the control for a distinction to familiarity may have been lacking. To show 'true' kin recognition, both genetic relatedness and familiarity must be controlled as independent factors (see below). For simplification in the following section we will refer to the term 'kin recognition' even if a genetic basis has not been proven. As the occurrence and relative importance of kin recognition mechanisms differ among taxa, we will review spiders and other arachnids separately in the following sections.

Sociality and Kin Recognition in Non-spider Arachnids

The degree of sociality in non-spider taxa varies greatly. While in harvestmen only gregarious behaviours are known (Chelini et al. 2012), some scorpion species can be regarded as subsocial as they show extended maternal care (Lourenço and Cloudsley-Thompson 2011). Mothers of the buthid scorpion *Tityus neblina* care for their young by protecting them and providing them with food. Other (non-buthid) species build communal nests, hunt cooperatively and feed communally (Shivashankar 1994). However, these associations are only temporary, and permanent sociality is not known for this arachnid group (Lourenço and Cloudsley-Thompson 2011). Kin recognition abilities may be present in scorpions. Mahsberg (1990) found in choice experiments that lab-raised juveniles of the subsocial scorpion *Pandinus imperator* prefer to associate with their own mother rather than with an unrelated female. Yet aggression against non-kin individuals has been reported to be very low (Mahsberg 1990). The result of the study of Mahsberg (1990), however, can also be explained by familiarity (cf. categories in Table 7.1) because prior to the experiments the juvenile scorpions stayed with their mother until the second instar. This gave them time to familiarise, and the outcome of the choice test may not necessarily mirror a preference based on genetic relatedness. In pseudoscorpions the situation seems very similar. Also here some species show subsocial behaviours that include nest cohabitation and food share until the offspring disperses (Del-Claro and Tizo-Pedroso 2009). Moreover, species of the genus *Paratemnoides* perform cooperative parental care, and in *P. nidificator* even a basic form of an age dependent division of labour has been suggested (Tizo-Pedroso and Del-Claro 2011). Kin recognition, however, has not yet been described. The only example of true kin recognition apart from spiders and mites (see below) comes from whip spiders (Amblypygi). Again, the evolutionary origin of their social interaction is an extension of maternal care (Rayor and Taylor 2006). For example, juveniles of *Phrynus marginemaculatus* and *Damon*

Table 7.1 The Knowns and unknowns about kin and nest mate recognition in arachnids

Affected traits	Taxon					
	Pseudoscorpiones	Scorpiones	Acari	Opiliones	Amblypygi	Araneae
Recognition based on familiarity						
Increased investigation	x	x	*Phytoseiulus persimilis*[17]	x	x	*Delena cancerides*[20]
Preferred association	x	*Pandinus imperator*[7]	x	x	x	Anelosimus eximius[8*] Stegodyphus lineatus[6]
Preferrential cannibalism	x	x	*Phytoseiulus persimilis*[12,13,14]	x	x	*Delena cancerides*[1*,10] *Diaea ergandros*[4] *Hogna helluo*[9] *Stegodyphus lineatus*[2]
Improved defence	x	x	*Phytoseiulus persimilis*[18]	x	x	x
Improved feeding efficiency through association with kin	x	x	*Phytoseiulus persimilis*[17,21]	x	x	*Stegodyphus lineatus*[15]
Recognition based on genetic cues						
Preferred association	x	x	x	x	*Damon diadema*[19]	x
Preferrential oviposition	x	x	*Iphiseius degenerans*[5]	x	x	x
Preferrential maternal feeding	x	x	x	x	x	*Diaea ergandros*[3]
Preferrential cannibalism	x	x	*Phytoseiulus persimilis*[12,13,14] *Phytoseiulus macropilis*[14]	x	*Damon diadema*[19]	x
Improved feeding efficiency through association with kin	x	x	x	x	x	*Stegodyphus lineatus*[15] *Stegodyphus tentoriicola*[11]

Several studies found individual recognition abilities without unravelling whether it is based on genetic relatedness or familiarity. We thus list the literature in two categories of 'kin recognition'. However, it might be shown in future investigations that some species assigned to 'familiarity' may in fact also possess kin recognition based on genetically based cues

Studies we indicated with "*" refer to nestmate recognition not specifically revealing or addressing genetic relatedness

References: (1) Beavis et al. (2007), (2) Bilde and Lubin (2001), (3) Evans (1998), (4) Evans (1999), (5) Faraji et al. (2000), (6) Johannesen and Lubin (2001), (7) Mahsberg (1990), (8) Mailleux et al. (2008), (9) Roberts et al. (2003), (10) Rowell and Avilés (1995), (11) Ruch et al. (2009), (12) Schausberger (2005), (13) Schausberger (2007), (14) Schausberger and Croft (2001), (15) Schneider (1996), (16) Schneider and Bilde (2008), (17) Strodl and Schausberger (2012a), (18) Strodl and Schausberger (2012b), (19) Walsh and Rayor (2008), (20) Yip et al. (2009), (21) Zach et al. (2012)

diadema stay with their mother for at least one year until they become solitary. In *D. diadema,* mothers and her offspring further show active aggregation under increased predation risk (Rayor and Taylor 2006). As the mentioned species show no cooperative prey capture or food share, the function of group living is most likely protection. Despite the lack of cooperation, kin recognition has been found in immature individuals of *D. diadema* (Walsh and Rayor 2008). In Y-maze choice tests, Walsh and Rayor (2008) showed that immature individuals are able to recognise their mother. Recognition is probably based on olfactory cues, as amblypygids are very sensitive to odours (Hebets and Chapman 2000), and tactile stimuli, as they use their 'whips' (first pair of legs) to physically contact conspecifics (Rayor and Taylor 2006). One hypothesis for the significance of immature kin recognition is that remembrance of siblings in the adult stage may serve to avoid serious injuries during fight, because adult whip spiders behave aggressively when they encounter potential conspecific competitors (Walsh and Rayor 2008).

The large arachnid group of mites (Acari) is trophically diverse, comprising vegetarian, predaceous and parasitic specialists. The sociality levels cover the whole range from solitary to subsocial and permanently social species that build large colonies with overlapping generations and even bi-parental brood care (Sato et al. 2003). Kin recognition has been revealed for various species but has not (yet) been found in the group of highly social spider mites. The advantages of group living in mites include reduction of evaporative water loss (Glass et al. 1998), increased foraging efficiency (Strodl and Schausberger 2012a) and increased survival by cooperative defence against predators (Mori and Saito 2005; Strodl and Schausberger 2012b). The latter is particularly evident for species that build common nests (Mori and Saito 2004, 2005). Even inherently solitary species, like the house dust mite *Dermatophagoides pteronyssimus*, sometimes form groups. When certain individuals start to migrate to new food patches they lay trails of chemical cues that attract conspecifics to follow (Mailleux et al. 2011). Hence, the migration becomes a collective phenomenon. Moving in a group may help to reduce dehydration risk, but interactions between individuals are lacking (Mailleux et al. 2011). Non-social predatory mites naturally show no expression of cooperation, but some species possess kin recognition abilities. Females of *Iphiseius degenerans* oviposit preferably next to eggs laid by related females rather than unrelated ones (Faraji et al. 2000). This behaviour is suggested to reduce the risk of kin cannibalism among juveniles once they will have hatched, as young are less likely to cannibalize relatives. In *P. persimilis* and *P. macropilis,* adult females tend to prey upon juvenile conspecifics with a significant preference for unrelated individuals (Schausberger and Croft 2001). Both species show no social behaviours and yet the authors discuss the adaptive significance of their kin discrimination abilities in context of inclusive fitness theory. In the case of a recognition error, females would experience a loss of inclusive fitness by eating related individuals (Schausberger and Croft 2001). Moreover, reducing the number of unrelated offspring by increased predation will finally relieve the young from intraspecific competition for food. This particular example refers to a recognition mechanism that might be the direct result of kin selected behaviours, however, Schausberger

(2007) later revealed that in *P. persimilis* kin recognition is an amazingly complex, context-dependent process. While these mites use genetically determined recognition cues, discrimination is nevertheless based on familiarity. An association early in life will reduce cannibalistic behaviours against familiar individuals in later juvenile stages, irrespective of whether they are kin or non-kin. Staying in a group of familiar individuals increases foraging efficiency (Strodl and Schausberger 2012a; Zach et al. 2012) and reduces response time to predatory attacks (Strodl and Schausberger 2012b), which is suggested to be mediated by the reduced time needed for the assessment of conspecifics (Strodl and Schausberger 2012a, b). The advantage of a familiarity-based recognition mode in *P. persimilis* is that it allows mothers to lay eggs next to clutches of unrelated females, and still juvenile cannibalism after hatching remains low (Schausberger 2007). Interestingly, the same species is also capable of 'true' kin recognition based on phenotype matching. Although the cannibalism rate is generally higher towards unfamiliar individuals, Schausberger (2007) demonstrated in a choice experiment that under food deprivation protonymphs prefer to cannibalise sibling larvae over non-sibs irrespective of the degree of familiarity. This latter behaviour is suggested to represent a selfish action to avoid competition of related alleles and to increase direct fitness (Schausberger 2007). Nevertheless, those benefits must be enormous for kin cannibalism to be adaptive given the cost of losing inclusive fitness, and may include an inbreeding avoidance strategy. Alternatively, kin cannibalism may also result from preferential association with kin and thus a by-product occurrence of early cannibalism on related individuals without indicating a true preference (see also Schausberger 2005). The example of predatory mites nicely illustrates that kin recognition also occurs in non-social species and that both processes, kin recognition based on genetic relatedness and familiarity, appear to be important in social interactions among various mite species.

Spider mites are considered as pest on crops (Saito 1987) yet showing high level of sociality. Apart from building permanent nests with overlapping generations, cooperation in nest construction, nest sanitation (Sato et al. 2003) and nest defence (Mori and Saito 2005) some species even perform bi-parental brood care (Saito 1987) which might be related to their genomic structure. While arachnids are typically diploid, some social spider mites are characterised by haplodiploidy which adds a particularly interesting aspect to the function of kin recognition. Similar to eusocial hymenopteran insects females of these mites produce haploid males (from unfertilised eggs) and diploid females. Despite the fact that in social spider mites no reproductive division of labour exists (Mori and Saito 2006), colonies are often founded by single females. The within-colony relatedness can be high, because a highly female biased sex ratio of the offspring has also been reported [e.g. *Tetranychus urticae* and *Schizotetranychus celaris*, Saito (1987); *Stigmaeopsis longus* and *S. miscanthi*, Sato and Saito (2007)]. Through mother-son matings the relatedness within a colony can be further increased, as it is the case in *S. celaris* (Acari, Tetranychidae). This mating behaviour may explain the unusual occurrence of paternal brood care, since in this inbreeding scenario the offspring has a much higher relatedness to the father than they would have if the father mated with a female from a foreign colony (Saito 1986, 1987). Kin recognition could be beneficial in order to maintain this male-offspring-relatedness by preferential matings with related females, but it has not been revealed for any permanently social mite species so far. Moreover, despite the complexity of social behaviours and a haplo-diploid system, Mori and Saito (2006) could neither find division of labour nor casts in *Schizotetranychus*.

Kin Recognition in Subsocial Spiders

Kin recognition in spiders is tightly linked with sociality and has not yet been found in solitary species (excluding species with extended maternal care as a form of sub-social behaviour). This might well be an artefact of a biased investigation, but it may also underpin the importance of kin recognition to facilitate the evolution of sociality in these animals. In spiders, kin recognition mechanisms are subtle and comprise a number of specific behaviours that are often highly context-dependent (Yip and Rayor 2014). Those mechanisms may be used to direct help towards related individuals in social groups or to discriminate against foreigners. *Delena cancerides*, a social huntsman species of the family Sparassidae, has reached a unique discrimination level. Colonies in this species may comprise up to 300 individuals that form social nests under the bark of trees, and in contrast to all other social arachnids, they behave aggressively towards individuals from foreign colonies (Rowell and Avilés 1995). Chemical cues may be used by the individually hunting spiders to find back to their own colonies. Those cues would also mark the home nest, and with it all inhabiting spiders, and may thus be used for nest mate recognition (see Rowell and Avilés 1995). In the permanently social *Anelosimus eximius* (Theridiidae), Pasquet et al. (1997) showed that volatile and non-volatile cuticular substances vary considerably among colonies. However, introduction of individuals from foreign colonies with different ‘odours’ did not appear to elicit measurable behavioural changes like increased aggression. This result, that differs from *D. cancerides*, may be related to the rather static nature of group living in *A. eximius*, as there is almost no individual exchange between colonies and thus direct competition among colonies over resources is rather weak (Pasquet et al. 1997). Moreover, social spiders tend to include foreigners in their colony because of benefits for survival, and selection against such inclusion is low despite the fact that large colonies may also experience higher intraspecific competition. Accordingly, it has been shown in *A. eximius* as well as in the social *S. dumicola* (Erisidae) that larger nests survive better than smaller ones (Avilés and Tufiño 1998; Bilde et al. 2007). In *D. cancerides* individuals are free hunting and more mobile, and therefore colonies are more often faced with wandering immigrants (Yip et al. 2012). They may be forced to actively maintain colony integrity, especially if colony retreats represent a limited resource (Yip et al. 2009). Interestingly, although sociality in *D. cancerides* is also suggested to originate from extended maternal care, colonies also comprise a substantial proportion of unrelated individuals. Thus, the pronounced discrimination against foreigners is based on both kin and non-kin nest mate recognition (Rowell and Avilés 1995). Is has subsequently been shown that true kin recognition exists in this species (Beavis et al. 2007). For a long time, it was unknown how the high level of intolerance towards immigration of unrelated individuals could result in mixed colony compositions, which is important to maintain outbreeding opportunities. Beavis et al. (2007) eventually found that adult females that founded a colony are reasonable tolerant towards juveniles with carapace width of less than 6 mm (see also Yip et al. 2009). Thus, juvenile dispersal may be the only way in this species to join groups of unrelated spiders and to maintain an outbred population structure (Yip et al. 2012).

That true distinction between kin and non-kin might be of adaptive significance in arachnids was shown in studies on subsocial *S. lineatus* (Schneider 1996; Bilde and Lubin 2001; Schneider and Bilde 2008). Under low food conditions these spiders show increased cannibalism in groups of unrelated individuals, which has been discussed in context of inclusive fitness maximisation (Bilde and Lubin 2001). Other studies revealed that subsocial *S. lineatus* also perform better when they forage in groups of siblings instead of mixed associations (Schneider 1996; Schneider and Bilde 2008). Kin groups fed more efficiently by extracting more food from the prey and grew at a higher rate. Schneider and Bilde (2008) used cross fostering experiments to prove that genetic relatedness and not familiarity among colony members improved the performance in *S. lineatus*. This study did not detect the mechanisms of kin recognition, but it was later shown that kin recognition in *S. lineatus* may be mediated by cuticle hydrocarbons (Grinsted et al. 2011). The behavioural or physiological mechanisms of kin discrimination in communal feeding events, however, are still unknown. Perhaps, these spiders invest differentially in digestive enzyme production and/or contribution to the extra-oral digestion when foraging with either kin or non-kin. Beyond an ‘optimal’ group size, further individuals that join will increase competition over food and the incentive for cheating (Whitehouse and Lubin 2005). Accordingly, Ruch et al. (2009) found that feeding efficiency decreases with increasing group size in subsocial *Stegodyphus tentoriicola*. This effect, however, is less pronounced in sibling groups and thus indicates a potential advantage of discriminating against non-kin when forming groups. The different feeding efficiency might be related to a dissimilar investment in releasing digestive enzymes (Ruch et al. 2009). As the production of digestive fluids is costly (Secor 2003) the motivation not to contribute own enzymes, and thus to cheat, may be enhanced in mixed groups. Nevertheless, cooperation can be maintained despite cheating if a single individual is unlikely to successfully monopolise a resource (Lubin and Bilde 2007). However, cheating creates a social dilemma as related individuals lose indirect fitness benefits (Schneider and Bilde 2008).

Cooperation may conflict with competition among members of a colony, for example over the best feeding-positions, the greatest share of captured prey items, or mating partners etc. Competition increases with increasing group size, which leads to a reduction in per capita fitness (Bilde et al. 2007). Under these conditions cheating becomes a tempting strategy (Lubin and Bilde 2007). Individuals may decide not to contribute to prey capture or web construction although taking advantage of both, or they may not contribute in producing and releasing digestive fluids while feeding communally. Following the theory of ‘the tragedy of the commons’ (Hardin 1968) selfish actions reduce the benefits of cooperation for other group members. Kin recognition may help to reduce negative effects of selfish actions because interacting with related individuals increases the cost of cheating by reducing inclusive fitness (Schneider and Bilde 2008). A preference for associating with kin may reduce the level of cheating and thus underpins the significance of kin recognition for the evolution of cooperation and the transition to permanently social spider societies (Lubin and Bilde 2007).

In the thomisid subsocial spider *Diaea ergandros*, Evans (1999) showed that the performance of sibling groups does not significantly differ from groups of unrelated individuals in the adult stage. Juveniles, however, contribute more to nest construction when cooperating with siblings, and if unfavourable conditions causes the colony to starve, cannibalism spreads and spiders then prefer to eat non-sibs first (Evans 1999). This would conform to kin-selection theory. However, the discrimination modes turned out to be complex. Starving subadult females would prefer to cannibalise foreign females but related males. This differential response was attributed to facilitation of outbreeding opportunities (Evans 1999; see also Johannesen and Lubin 1999).

Kin Recognition and Permanent Sociality in Spiders

It is evident that kin recognition is favoured by inclusive fitness benefits, and most likely kin cooperation plays a role in the transition to permanent sociality in spiders. So far, kin recognition has not been found in permanently social spiders. Perhaps, once permanent sociality has evolved, there may be additional selective forces that maintain cooperation. For example, high and predictable genetic relatedness among group members may relax selection for maintaining kin recognition (Lubin and Bilde 2007; Yip and Rayor 2014). Also, mutualistic benefits of cooperation (see Kokko et al. 2001) and infrequent encounters with competing groups would reduce the need for a kin recognition system (Waldman 1988). These conditions characterise permanently social spiders, that are severely inbred with low intra-colony genetic variation (Lubin and Bilde 2007), and group augmentation increases colony survival (Avilés and Tufiño 1998; Bilde et al. 2007). Indeed, the scarce evidence for kin discrimination and nepotism in permanently social species support relaxed selection for these traits, and it is therefore possible that they have been lost with the transition from subsocial to permanently social living (Lubin and Bilde 2007; Berger-Tal et al. 2015). This observation underlines that kin recognition in spiders and other arachnids is not an obligate prerequisite for the maintenance of group living and cooperation. However, social spiders may well benefit from kin selected traits that led to their level of cooperation. If they gain both inclusive fitness from allo-maternal care, and direct fitness from increased survival of larger groups, this is sufficient to explain the maintenance of cooperation. An alternative explanation, the principle of reciprocity (Axelrod and Hamilton 1981), requires score-keeping, individual recognition and repeated interactions amongst individuals. While this could in principle happen, by-product mutualism (Eberle and Kappeler 2008) would be more likely to explain direct benefits of cooperation in spiders.

Kin Recognition Cues

Kin recognition has been demonstrated in several spider species, whereas we have yet to understand the actual underlying recognition mechanisms. As shown above, for interspecific recognition mechanisms, spiders use tactile chemical cues to regulate their interactions. Chemicals deposited on silk are well known to serve as effective cues (Seibt and Wickler 1988; Evans and Main 1993), but have not yet been revealed to play a role in kin recognition. For example, *S. lineatus* is able to recognise the silk of its own species, but individuals do not show any preference for the silk of kin or non-kin (Bilde et al. 2002). In eusocial insects, cuticular hydrocarbons have been identified to convey specific information about the colony identity or the degree of relatedness (Lahav et al. 1999; Dani et al. 2005; d'Ettorre and Moore 2008). Hence, it seems reasonable to screen other arthropods for similar mechanisms. Grinsted et al. (2011) finally found evidence for cuticular hydrocarbons also mediating kin recognition in the subsocial spider *S. lineatus*. The hydrocarbon profiles of juvenile pre-dispersal spiders vary considerably, thus potentially carrying information about the family identity that can be used for kin discrimination. Behavioural experiments further demonstrated that the spiders preferably choose to reside next to cuticular chemical extracts of siblings (Grinsted et al. 2011). Moreover, the composition of branched alkanes as a subset of identified hydrocarbons is not substantially influenced by environmental factors underpinning a genetic basis of the substance makeup to be used as cues. Direct fitness benefits of cooperating with kin (see. Schneider 1996; Schneider and Bilde 2008) may have favoured selection towards using these cuticular substances as a kin recognition tool.

Summary

This overview reveals that social recognition abilities exist in various social and non-social arachnids. It allows individuals to distinguish between congeners, conspecifics, nestmates, and related and unrelated individuals to either support or discriminate against them. Interestingly, kin recognition also occurs in species that do not form groups. However, it is always linked to social interactions, at least in juvenile associations. The adaptive significance of these social behaviours resides in functions like increased protection, foraging efficiency and brood care and true cooperation in foraging, predator defence and cooperative breeding. However, the role of kin recognition as a mediator for these behaviours remains understudied.

In contrast to the eusocial insects, where kin recognition mediates both within- and between-colony interactions, the adaptive value of kin recognition in arachnids appears to be more context-dependent. It varies among species with differing sociality levels and life stages. Yet, kin recognition is accepted to have fitness benefits and has been suggested to play a role in the transition from subsocial to social living by promoting close kin associations. Possessing the ability to recognise and discriminate kin is particularly valuable for species that frequently interact with non-kin as it occurs in many subsocial species. By contrast, interactions with non-kin are rare in social species and thus selection may not favour the maintenance of recognition abilities. Accordingly, kin recognition has not been demonstrated in permanently social species yet.

The adaptive significance of kin recognition may be hard to discern, but sometimes it might simply be behaviourally undetectable. For example, the advantage of cooperation among related spiders might reside in performance differences in communal feeding events on a molecular level. Either individual spiders could contribute more or less digestive enzymes depending on who they are feeding with, or the digestive fluids of non-kin could be less compatible than those of kin. Through immunological differences, the enzymes themselves may compete inside the carcass of the prey resulting in a reduced effectiveness of the extra oral digestion in non-kin feeding groups. Here, the adaptive significance of kin recognition and kin discrimination may be very subtle. It might only manifest in the form of preferential association with kin for feeding. Thus, apart from simply detecting kin discrimination in particular species, future studies may need to screen more closely for specific contexts in which this ability appears to be adaptive. This has been exemplarily done in studies on preferential cannibalism among juveniles, but may be extended to other scenarios that influence the performance of groups, like foraging, feeding, brood care, defence etc. Another open question that needs to be answered in future investigations is the importance of kin recognition abilities for the transition from subsociality to permanently social group living. For that, we need to identify and to focus on transitional species to unravel crucial kin-selected trait(s) that facilitate the formation of permanent colonies. One of the key issues will be a better understanding of the recognition mechanisms and a clear distinction between the use of genetically based recognition cues and familiarity. Uncovering the evolutionary importance of social recognition in arachnids turns out to be a puzzle, generalisations may not be possible, and only a stepwise approach can provide us with a more comprehensive knowledge of their sociality.

References

Agnarsson I (2002) Sharing a web—on the relation of sociality and kleptoparasitism in theridiid spiders (Theridiidae, Araneae). J Arachnol 30:181–188

Agnarsson I, Avilés L, Coddington JA, Maddison WP (2006) Sociality in theridiid spiders: repeated origins of an evolutionary dead end. Evolution 60:2342–2351

Anthony CD (2003) Kinship influences cannibalism in the wolf spider, *Pardosa milvina*. J Insect Behav 16:23–36

Assi-Bessékon D, Horel A (1996) Social-maternal relations in *Coelotes terrestris* (Araneae, Agelenidae): influence of the female reproductive state on its tolerance towards conspecific spiderlings. Behav Process 36:19–26

Avilés L (1997) Causes and consequences of cooperation and permanent sociality in spiders. In: Choe JC, Crespi BJ (eds) The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge, pp 476–498

Avilés L, Tufiño P (1998) Colony size and individual fitness in the social spider *Anelosimus eximius*. Amer Nat 152:403–418

Axelrod R, Hamilton WD (1981) The evolution of cooperation. Science 211:1390–1396

Beavis AS, Rowell DM, Evans T (2007) Cannibalism and kin recognition in *Delena cancerides* (Araneae: Sparassidae), a social huntsman spider. J Zool 271:233–237

Berger-Tal R, Lubin Y, Bilde T, Settepani V, Majer M, Tuni C (2015) Evidence for loss of nepotism in the evolution of permanent sociality. Nature Scientific Reports

Bessékon DA (1997) Intraspecific identification and tolerance in the social-maternal behaviour of *Coelotes terrestris* (Araneae, Agelenidae). Behav Proc 39:231–239

Bilde T, Lubin Y (2001) Kin recognition and cannibalism in a subsocial spider. J Evolution Biol 14:959–966

Bilde T, Lubin Y (2011) Group living in spiders: cooperative breeding and coloniality. In: Herberstein ME (ed) Spider behaviour: flexibility and versatility. Cambridge University Press, Cambridge, pp 275–307

Bilde T, Maklakov AA, Taylor PW, Lubin Y (2002) State-dependent decisions in nest site selection by a web-building spider. Anim Behav 64:447–452

Bilde T, Coates KS, Birkhofer K, Maklakov AA, Lubin Y, Avilés L (2007) Survival benefits select for group living in a social spider despite reproductive costs. J Evolution Biol 20:2412–2426

Boomsma JJ (2007) Kin selection versus sexual selection: why the ends do not meet. Curr Biol 17:673–683

Bowden K, Jackson RR (1988) Social organisation of *Scytodes fusca*, a communal web-building spitting spider (Araneae, Scytodidae) from Queensland. New Zeal J Zool 15:365–368

Brach V (1975) The biology of the social spider *Anelosimus eximius* (Araneae: Theridiidae). Bull So Calif Acad Sci 74:37–41

Brach V (1977) *Anelosimus studiosus* (Araneae: Theridiidae) and the evolution of quasisociality in theridiid spiders. Evolution 31:154–161

Buskirk RE (1981) Sociality in the arachnida. In: Hermann HR (ed) Social insects, vol II. Academic Press, New York pp 281–367

Chelini M-C, Willemart RH, Gnaspini P (2012) Gregarious behavior of two species of Neotropical harvestmen (Arachnida: Opiliones: Gonyleptidae). J Arachnol 40:256–258

Clotuche G, Deneubourg J-L, Mailleux A-C, Detrain C, Hance T (2012) Discrimination through silk recognition: the case of the two-spotted spider mite *Tetranychus urticae*. C R Biol 335:535–540

d'Ettorre P, Moore AJ (2008) Chemical communication and the coordination of social interactions in insects. In: d'Ettorre P, Hughes DP (eds) Sociobiology of communication: an interdisciplinary perspective. Oxford University Press, Oxford, pp 81–96

Dani FR, Jones GR, Corsi S, Beard R, Pradella D, Turillazzi S (2005) Nestmate recognition cues in the honey bee: differential importance of cuticular alkanes and alkenes. Chem Senses 30:477–489

Del-Claro K, Tizo-Pedroso E (2009) Ecological and evolutionary pathways of social behaviour in Pseudoscorpions (Arachnida: Pseudoscorpiones). Acta Ethol 12:13–22

Eberle M, Kappeler PM (2008) Mutualism, reciprocity, or kin selection? Cooperative rescue of a conspecific from a boa in a nocturnal solitary forager the gray mouse lemur. Am J Primatol 70:410–414

Evans TA (1998) Offspring recognition by mother crab spiders with extreme maternal care. Proc R Soc Lond B 265:129–134

Evans TA (1999) Kin recognition in a social spider. Proc R Soc Lond B 266:287–292

Evans TA, Main BY (1993) Attraction between social crab spiders: silk pheromones in *Diaea socialis*. Behav Ecol 4:10–99

Faraji F, Janssen A, van Rijn PCJ, Sabelis MW (2000) Kin recognition by the predatory mite *Iphiseius degenerans*: discrimination among own, conspecific and heterospecific eggs. Ecol Entomol 25:147–155

Glass EV, Yoder JA, Needham GR (1998) Clustering reduces water loss by adult American house dust mites *Dermatophagoides farinae* (Acari: Pyroglyphidae). Exp Appl Acarol 22:31–37

Griffin AS, West SA (2003) Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. Science 302:634–636

Grinsted L, Bilde T (2013) Effects of within-colony competition on body size asymmetries and reproductive skew in a social spider. J Evolution Biol. doi:10.1111/jeb.12072

Grinsted L, Bilde T, d'Ettorre P (2011) Cuticular hydrocarbons as potential kin recognition cues in a subsocial spider. Behav Ecol 22:1187–1194

Grinsted L, Agnarsson I, Bilde T (2012) Subsocial behaviour and brood adoption in mixed-species colonies of two theridiid spiders. Naturwissenschaften 99:1021–1030

Grinsted L, Pruitt JN, Settepani V, Bilde T (2013) Individual personalities shape task differentiation in a social spider. Proc R Soc Lond B. doi:10.1098/rspb.2013.1407

Gundermann JL, Horel A, Krafft B (1993) Experimental manipulations of social tendencies in the subsocial spider *Coelotes terrestris*. Insect Soc 40:219–229

Hamilton WD (1964) The genetical evolution of social behaviour I and II. J Theor Biol 7:1–16, 17–52

Hardin G (1968) The tragedy of the commons. Science 162:1243–1248

Hebets EA, Chapman RF (2000) Electrophysiological studies of olfaction in the whip spider *Phrynus parvulus* (Arachnida, Amblypygi). J Insect Physiol 46:1441–1448

Henschel JR (1998) Predation on social and solitary individuals of the spider *Stegodyphus dumicola* (Araneae, Erisidae). J Arachnol 26:61–69

Jackson RR (1982) Comparative studies of Dictynia and Mallos (Araneae: Dictynidae): IV. Silk-mediated interaction. Insect Soc 29:15–24

Johannesen J, Lubin Y (1999) Group founding and breeding structure in the subsocial spider *Stegodyphus lineatus* (Erisidae). Heredity 82:677–686

Johannesen J, Lubin Y (2001) Evidence for kin-structured group founding and limited juvenile dispersal in the sub-social spider *Stegodyphus lineatus* (Araneae, Erisidae). J Arachnol 29:413–422

Johannesen J, Lubin Y, Smith DR, Bilde T, Schneider JM (2007) The age and evolution of sociality in *Stegodyphus* spiders: A molecular phylogenetic perspective. Proc R Soc B 274:231–237

Kim KW (2000) Dispersal behaviour in a subsocial spider: Group conflict and the effect of food availability. Behav Ecol Sociobiol 48:182–187

Kokko H, Johnstone RA, Clutton-Brock T (2001) The evolution of cooperative breeding through group augmentation. Proc R Soc B 268:187–196

Kullmann E (1968) Soziale Phaenomene bei Spinnen. Insect Soc 3:289–298

Kullmann EJ (1972) Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). Am Zool 12:419–426

Lahav S, Soroker V, Hefetz A, Vander Meer RK (1999) Direct behavioral evidence for hydrocarbons as ant recognition discriminators. Naturwissenschaften 86:246–249

Lourenço WR, Cloudsley-Thompson JL (2011) Aspects of maternal care and social behaviour in scorpions; *Tityus* (*Atreus*) *neblina* Lourenço (Scorpiones, Buthidae). Boletín de la Sociedad Entomológica Aragonesa 49:291–293

Lubin Y, Bilde T (2007) The evolution of sociality in spiders. In: Brockmann HJ, Roper TJ, Naguib M, Wynne-Edwards KE, Barnard C, Mitani J (eds) Advances in the study of behavior, vol 37. Elsevier, Amsterdam, pp 83–145

Machado G, Macías-Ordoñez R (2007) Social behavior. In: Pintoda-Rocha R, Machado G, Giribet G (eds) Harvestmen. The biology of Opiliones. Harvard University Press, Cambridge, pp 400–413

Mahsberg D (1990) Brood care and family cohesion in the tropical scorpion *Pandinus imperator* (Koch) (Scorpiones: Scorpionidae). Acta Zool Fennica 190:267–272

Mailleux A-C, Furey R, Saffre F, Krafft B, Deneubourg J-L (2008) How non-nestmates affect the cohesion of swarming groups in social spiders. Insect Soc 55:355–359

Mailleux A-C, Astudillo Fernandez A, Martin GS, Detrain C, Deneubourg J-L (2011) Collective migration in house dust mites. Ethology 117:72–82

Majer M, Agnarsson I, Svenning JC, Bilde T (2013a) Social species of the spider genus *Anelosimus* occur in wetter, more productive habitats than non-social species. Naturwissenschaften. doi:10.1007/s00114-013-1106-6

Majer M, Svenning JC, Bilde T (2013b) Habitat productivity constrains the distribution of social spiders across continents—case study of the genus *Stegodyphus*. Front Zool. doi:10.1186/1742-9994-10-9

Maynard Smith J (1964) Group selection and kin selection. Nature 201:1145–1147

Mori K, Saito Y (2004) Nest-size variation reflecting anti-predator strategies in social spider mites of *Stigmaeopsis* (Acari: Tetranychidae). Behav Ecol Sociobiol 56:201–206

Mori K, Saito Y (2005) Variation in social behavior within a spider mite genus, *Stigmaeopsis* (Acari: Tetranychidae). Behav Ecol 16:232–238

Mori K, Saito Y (2006) Communal relationships in a social spider mite, *Stigmaeopsis longus* (Acari: Tetranychidae): an equal share of labor and reproduction between nest mates. Ethology 112:134–142

Nentwig W (1985) Social spiders catch larger prey: a study of *Anelosimus eximius* (Araneae: Theridiidae). Behav Ecol Sociobiol 17:79–85

Pasquet A, Trabalon M, Bagnères AG, Leborgne R (1997) Does group closure exist in the social spider *Anelosimus eximius*? Behavioural and chemical approach. Insect Soc 44:159–169

Plateaux-Quènu C, Horel A, Roland C (1997) A reflection on social evolution in two different groups of arthropods: Halictine bees (Hymenoptera) and spiders (Arachnida). Ethol Ecol Evol 9:183–196

Polis GA, Lourenço WR (1986) Sociality among scorpions. Actas X Congreso Internacional de Aracnologia, Jaca/España 1:111–115

Powers KS, Avilés L (2007) The role of prey size and abundance in the geographical distribution of spider sociality. J Anim Ecol 76:995–1003

Rayor LS, Taylor LA (2006) Social behavior in amblypygids, and a reassessment of arachnid social patterns. J Arachnol 34:399–421

Roberts JA, Taylor PW, Uetz GW (2003) Kinship and food availability influence cannibalism tendency in early-instar wolf spiders (Araneae: Lycosidae). Behav Ecol Sociobiol 54:416–422

Rowell DM, Avilés L (1995) Sociality in a bark-dwelling huntsman spider from Australia, *Delena cancerides* Walckenaer (Araneae: Sparassidae). Insect Soc 42:287–302

Ruch J, Heinrich L, Bilde T, Schneider JM (2009) Relatedness facilitates cooperation in the subsocial spider, *Stegodyphus tentoriicola*. BMC Evol Biol. doi:10.1186/1471-2148-9-257

Saito Y (1986) Biparental defence in a spider mite (Acari: Tetranyehidae) infesting *Sasa* bamboo. Behav Ecol Sociobiol 18:377–386

Saito Y (1987) Extraordinary effects of fertilization status on the reproduction of an arrhenotokus and sub-social spider mite (Acari: Tetranychidae). Res Popul Ecol 29:57–71

Samuk K, Avilés L (2013) Indiscriminate care of offspring predates the evolution of sociality in alloparenting social spiders. Behav Ecol Sociobiol 67:1275–1284

Sato Y, Saito Y (2007) Can the extremely female-biased sex ratio of the social spider mites be explained by Hamilton's local mate competition model? Ecol Entomol 32:597–602

Sato Y, Saito Y, Sakagami T (2003) Rules for nest sanitation in a social spider mite, *Schizotetranychus miscanthi* Saito (Acari: Tetranychidae). Ethology 109:713–724

Schausberger P (2005) The predatory mite *Phytoseiulus persimilis* manipulates imprinting among offspring through egg placement. Behav Ecol Sociobiol 58:53–59

Schausberger P (2007) Kin recognition by juvenile predatory mites: prior association or phenotype matching? Behav Ecol Sociobiol 62:119–125

Schausberger P, Croft BA (2001) Kin recognition and larval cannibalism by adult females in specialist predaceous mites. Anim Behav 61:459–464

Schneider JM (1995) Survival and growth in groups of a subsocial spider (*Stegodyphus lineatus*). Insect Soc 42:237–248

Schneider JM (1996) Food intake, growth and relatedness in the subsocial spider, S*tegodyphus lineatus* (Eresidae). Ethology 102:386–396

Schneider JM (2002) Reproductive state and care giving in *Stegodyphus* (Araneae: Eresidae) and the implications for the evolution of sociality. Anim Behav 63:649–658

Schneider JM, Bilde T (2008) Benefits of cooperation with genetic kin in a subsocial spider. Proc Natl Acad Sci USA 105:10843–10846

Secor SM (2003) Gastric function and its contribution to the postprandial metabolic response of the Burmese python *Python molurus*. J Exp Biol 206:1621–1630

Seibt U, Wickler W (1987) Gerontophagy versus cannibalism in the social spiders *Stegodyphus mimosarum* Pavesi and *Stegodyphus dumicola* Pocock. Anim Behav 35:1903–1905

Seibt U, Wickler W (1988) Interspecific tolerance in social *Stegodyphus* spiders (Erisidae, Araneae). J Arachnol 16:35–39

Settepani V, Grinsted L, Granfeldt J, Jensen JL, Bilde T (2013) Task specialization in two social spiders, *Stegodyphus sarasinorum* (Eresidae) and *Anelosimus eximius* (Theridiidae). J Evolution Biol. doi:10.1111/jeb.12024

Sherman PW, Reeve HK, Pfennig DW (1997) Recognition systems. In: Krebs JR, Davies NB (eds) Behavioural Ecology: an evolutionary approach, 4th edn. Blackwell Scientific, Oxford, pp 69–96

Shivashankar T (1994) Advanced sub social behaviour in the scorpion *Heterometrus fulvipes* Brunner (Arachnida). J Biosci 19:81–90

Strodl MA, Schausberger P (2012a) Social familiarity reduces reaction times and enhances survival of group-living predatory mites under the risk of predation. PLoS ONE 7(8):e43590. doi:10.1371/journal.pone.0043590

Strodl MA, Schausberger P (2012b) Social familiarity modulates group living and foraging behaviour of juvenile predatory mites. Naturwissenschaften 99:303–311

Tizo-Pedroso E, Del-Claro K (2007) Cooperation in the Neotropical pseudoscorpion, *Paratemnoides nidificator* (Balzan, 1888): feeding and dispersal behaviour. Insect Soc 54:124–131

Tizo-Pedroso E, Del-Claro K (2011) Is there division of labor in cooperative pseudoscorpions? An analysis of the behavioral repertoire of a tropical species. Ethology 117:498–507

Trabalon M, Assi-Bessekon D (2008) Effects of web chemical signatures on intraspecific recognition in a subsocial spider, *Coelotes terrestris* (Araneae). Anim Behav 76:1571–1578

Uetz GW, Hieber CS (1997) Colonial web-building spiders: balancing the costs and benefits of group-living. In: Choe JC, Crespi BJ (eds) The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge, pp 458–475

Waldman B (1988) The ecology of kin recognition. Ann Rev Ecol Syst 19:543–571

Waldman B, Frumhoff PC, Sherman PW (1988) Problems of kin recognition. Trends Ecol Evol 3:8–13

Walsh RE, Rayor LS (2008) Kin discrimination in the amblypygid, *Damon diadema*. J Arachnol 36:336–343

Ward PI (1986) Prey availability increases less quickly than nest size in the social spider *Stegodyphus mimosarum*. Behaviour 97:213–225

Weygoldt P (1969) The biology of pseudoscorpions. Harvard University Press, Cambridge

Whitehouse MEA, Lubin Y (2005) The functions of societies and the evolution of group living: Spider societies as a test case. Biol Rev 80:347–361

Wickler W, Seibt U (1993) Pedogenetic sociogenesis via the "sibling-route" and some consequences for *Stegodyphus* spiders. Ethology 95:1–18

Wilson EO (1971) The insect societies. Cambridge, Belknap

Wright CM, Holbrook CT, Pruitt JN (2014) Animal personality aligns task specialization and task proficiency in a spider society. Proc Natl Acad Sci USA 111:9533–9537

Yip EC, Rayor LS (2014) Maternal care and subsocial behaviour in spiders. Biol Rev. doi:10.1111/brv.12060

Yip EC, Powers KS, Avilés L (2008) Cooperative capture of large prey solves scaling challenge faced by spider societies. P Natl Acad Sci USA 105:11818–11822

Yip EC, Clarke S, Rayor LS (2009) Aliens among us: Nestmate recognition in the social huntsman spider, *Delena cancerides*. Insect Soc 56:223–231

Yip EC, Rowell DM, Rayor LS (2012) Behavioural and molecular evidence for selective immigration and group regulation in the social huntsman spider, *Delena cancerides*. Biol J Linn Soc 106:749–762

Zach GJ, Peneder S, Strodl MA, Schaus P (2012) Social familiarity governs prey patch-exploitation,—leaving and inter-patch distribution of the group-living predatory mite *Phytoseiulus persimilis*. PLoS ONE 7(8):e42889. doi:10.1371/journal.pone.0042889

Chapter 8
Visual Recognition in Social Wasps

R. Cervo, A. Cini and S. Turillazzi

Abstract Social recognition, i.e. the ability to recognize and assign individual membership to a particular and relevant class, such as caste, dominance status, gender or colony, shapes the amazing organization of insect societies. Traditionally, it has been assumed that social recognition in social insects is mainly governed by chemicals. However, social insects also share information via many other sensory channels, and it has been recently demonstrated that visual signals can mediate several types of social recognition in some species of social wasps. Primitively social wasps, such as paper wasps of *Polistes* genus, are suitable models to investigate visual communication because their combs lack of envelops allowing light to produce visual cues, their colonies are small, they have a good vision, they show a remarkable individual within-colony colour variation and, finally, they show an intense social life based on social recognition. In this chapter we reviewed the role of visual cues in social recognition inside and outside social wasp colonies focusing both on the intraspecific and interspecific recognition contexts.

Introduction

Recognition ability is an essential requirement for social behavior. Social insect colonies are well integrated societies characterized by a high level of cooperation among colony members (Wilson 1971). Such complex social interactions

---

R. Cervo (✉) · A. Cini · S. Turillazzi
Dipartimento di Biologia, Università degli Studi di Firenze,
via Madonna del Piano, 6, 50019 Sesto Fiorentino, FI, Italy
e-mail: rita.cervo@unifi.it

A. Cini
Laboratoire Écologie & Évolution UMR 7625, Université Pierre et Marie Curie,
7 Quai St Bernard, 75005 Paris, France

L. Aquiloni and E. Tricarico (eds.), *Social Recognition in Invertebrates*,
DOI 10.1007/978-3-319-17599-7_8

are possible thanks to the continuous exchange of information among individuals. Indeed, all forms of response following social interactions depend on some types of recognition. For example, the ability to discriminate nestmates from non-nestmates allows each colony member to favor the self and at the same time to repel the non-self, thus making social insect colonies highly defended xenophobic fortresses (Van Zweden and d'Ettorre 2010). The amazing organization of a social insect colony is however based not only on nestmate recognition but more in general on the ability to recognize and assign individual membership to a particular and relevant class, such as caste, dominance status, gender and so on.

In many social insects, the combination of a high number of individuals per colony and the common tendency to nest in sheltered and dark places (e.g. soil or enveloped nests) has favored the evolution of a large repertoire of chemicals (pheromones) to mediate intra-colonial transfer of information. Traditionally, it has been assumed that social insect life is governed by chemicals (Howard and Blomquist 2005; see this book) although social insects can transfer information to their nestmates, conspecifics and heterospecifics also via many other different channels, including the acoustic (reviewed in Kirchener 1997), vibrational (reviewed in Hunt and Richard 2013) and visual one (e.g. Nieh 2004). However, since a few time ago, the cues involved in social recognition in bees, ants, termites and wasps have been believed to be almost exclusively the chemical ones, with the hydrocarbons that cover the insect cuticle playing a major role (Howard and Blomquist 2005; see this book).

Already one century ago Wilhelmine Enteman (quoted by Strassmann 2004) described the amazing colour variation within the members of a *Polistes* wasp colony, but only recently this variability suggested that also visual signals can be strongly involved in mediating several types of social recognition (Tibbetts 2002; Tibbetts and Dale 2004).

In this review we will discuss the influence of visual cues in social recognition in primitively social wasps that represent interesting models to investigate the functioning and evolution of visual recognition. Indeed, these societies are rather small, with poorly differentiated phenotypes and highly flexible (almost all individuals can become fertile and reproduce). More than simply aiding researchers in their experimental work, these features represent a favourable environment where a full range of different recognition systems can evolve, from individual recognition (IR) to status recognition. Moreover, contrary to many social insects that live in the darkness (underground as many ants or termites, or in enveloped nests such as bees and some more eusocial Vespinae), primitively social wasps such as *Polistes* and most Stenogastrinae live in open nests, where communication by using reflected light to produce visual signals is possible.

This review will focus on *Polistes* paper wasps, as the bulk of visual recognition studies (more than the 95 %) has been carried out in this genus. Nonetheless, we will discuss also available information on Stenogastrinae hover wasps, which recently raised attention as they can provide independent test on the evolution of visual recognition in a different social clade (Baracchi et al. 2013). The review will cover the importance of visual cues in mediating social recognition inside and outside social insect colonies, both in the intraspecific and interspecific context.

Status Recognition and Quality Signals

A paper published by Tibbetts and Dale on *Nature* magazine in November 2004 revolutionized what previously thought about the communication system in *Polistes* paper wasps. Basically, this study showed that differences in the black area on the yellow clypeus of female *Polistes dominula* make a variable facial pattern that conveys information about the competitive ability of an individual to potential opponents.

These conventional signals, also known as 'badges of status' (Smith and Harper 2003), have been largely studied in passerine birds (Rohwer 1975, 1977; Senar and Camerino 1998) and lizards (Whiting et al. 2003), where small patches of color on the body of each individual influence the outcome of contests over resources in a group. These signals, that are claimed to be the animal equivalent of sergeants' strips (Roper 1986), allow to reduce costs and injuries linked to overt fights (Smith and Harper 2003). Badges of status are generally considered to be 'conventional' signals as they are not causally linked to resource-holding potential and they have no production cost (Smith and Harper 1988). However, being cost free, they could be exploited by low quality individuals to cheat about their real quality. Theory predicts that social costs guarantee the honesty of 'badge of status' signals because the cheater benefits should be overwhelmed by increasing challenge by group mates (see Smith and Harper 1988).

In *Polistes* paper wasps contests typically occur in early Spring when inseminated females (foundresses) exit from their overwintering refuges and search for a place where start a new colony. In *P. dominula,* a model species for sociobiological studies (Starks et al. 2006), nest can be founded either by a single foundress or by a group of associate foundresses (Pardi 1948). Before nest foundation, foundresses typically engage in harsh fights to determine the rank position of each individual within a group. After this early period, aggression decreases and ritualized non-aggressive dominance interactions among co-foundresses on the nest determine a linear hierarchy (Pardi 1948). The dominance order mirrors the reproductive skew in the colony: the dominant foundress monopolizes reproduction and becomes the principal egg layer (more than 90 % of the eggs in a *P. dominula* nest belongs to the alpha female, Queller et al. 2000) while the subordinate foundresses, although potentially capable to reproduce, renounce to their direct fitness and engage in typically worker tasks as foraging, nest building, colony defense and brood care (Pardi 1948).

The potential conflict over nest ownership and reproduction among co-foundresses may have represented strong selective pressures driving the evolution of badge of status signals. Given their high variability, the markers on wasp faces may indeed represent good candidates, allowing individuals to quickly assess the agonistic abilities of potential rivals and minimizing the time and costs during the nest founding stage contests. Indeed, facial pattern variability of foundresses of *P. dominula* is remarkable, especially in some areas, such as in North America (where the species has been recently introduced from its native Eurasian range; Cervo et al. 2000; Liebert et al. 2006). The yellow clypeus can have one or more black spots or no black spots at all, and the size and the shape of the spots can be very variable (Fig. 8.1). In order to catch and quantify this variability, Tibbetts and Dale (2004) introduced a new index, called 'badge brokenness index', that represents a measure of pattern disruption (by calculating the standard deviation of amount of black pigment deposited along the horizontal gradient located between the two peaks).

If facial markers are badges of status, they should be linked to some individual quality feature (such as body size) and to social dominance. Indeed,

Species	**Areas and parameters investigated**
P. dominula	Area, shape, presence of black pigmented spots on the clypeus; Size and shape of the abdominal spot
P. fuscatus	Pattern of facial markings: eye stripes, eyebrows, clypeus pattern, abdominal stripes
P. exclamans	Width, lenght and area ofthe brown stripe on the clypeus
P.metricus	Pattern of facial markings: eye stripes, eyebrows,clypeus pattern, abdominal stripes
P. satan	Percentage of the black/brown painted area relative to the head area
P. sulcifer,	Presence/position of the black band on the clypeus
P. semenowi	Presence/position of the black band on the clypeus
L. flavolineata	Size of the brown pigmented area on the face
L. vechti	Size of the brown pigmented area on the face
P. melly	Number of white stripes on the abdominal tergites

Fig. 8.1 Variability in facial patterns in some *Polistes* and Stenogastrinae wasps and the areas investigated in each species. From *top* to *bottom*: *P. dominula, P. fuscatus*, *P. metricus*, *P. exclamans*, *P. satan*, *P. sulcifer*, *L. flavolineata*; photos of facial patterns of *P. semenowi*, *L. vectti* and *P. melly* are not shown. Photo credits E.A. Tibbetts (*P. fuscatus*, *P. exclamans*, *P. metricus*), F.S. Nascimento (*P. satan*), D. Baracchi (*L. flavolineata*)

brokenness index (as well as the number of spots and the percentage of clypeus black) positively correlated with body size and facial markers predicts social rank in laboratory dominance trials (Tibbetts and Dale 2004). Unfamiliar prefounding females with different facial pattern collected in the new invaded area of this species (Ithaca, New York) were paired for body size and their interactions where observed for two hours in an experimental arena: mean badge brokenness as well as number of spots (but not percentage of clypeus black) were slightly (see Strassmann 2004) higher in females that were dominant in the contest trials than in subordinate females. Moreover, the mount rate performed by alphas on betas, to reinforce their position in each pair after dominance was established, was positively correlated with the facial pattern of betas, indicating that subordinate foundresses received more aggression if they had badges associate with higher dominance (Tibbetts and Dale 2004). Finally, experimentally alterations of the badge of subordinate individuals, after hierarchy was established, by painting with a mark indicating a higher status than their real one (simulating cheaters) made them be punished by alphas. Overall, the results obtained by Tibbetts and Dale (2004) suggest that facial markers are signals of quality and that low rank individuals are prevented to cheat about their status, even though its signaling would appear to be cost free, by the social costs they would pay. In this way, honesty should be maintained as cheating subordinates would be punished. As pointed out by Strassmann (2004), it is surprising that no effects on behavior were observed when facial markers manipulation was performed before the establishment of the dominance order because by painting a female face with a higher status mark she should have had more chances to become dominant. However, the response to signals of agonistic ability are often reported to be context dependent also in birds; which may explain why sometimes wasp females with experimentally increased badges do not increase their social rank.

An expected consequence of the “badge of status hypothesis” is that the facial patterns of co-foundresses in wild associative foundations would predict the dominance order, i.e. dominant individuals would have more black spots and more ‘broken’ facial pattern than subordinate individuals. Surprisingly, Cervo et al. (2008) didn’t find any correlation between rank position and facial pattern (considering the number of spots, the percentage of black area and the brokenness index) by checking the visual markers of foundresses in wild spring foundations observed for dominance hierarchies in several Italian populations, i.e. in the native range of the species. Similar results were reported for an another native population of *P. dominula* in Spain (Zanette and Field 2009; Green et al. 2012). Such differences could be due to the low frequency of females with clypeus marks in the European studied populations in comparison with American one (Tibbetts and Dale 2004; Cervo et al. 2008; Zanette and Field 2009). This strictly geographic variation in signaling among different populations of this species (Tibbetts et al. 2011a, b; Green et al. 2012) suggests a possible association between facial pattern and climate. Wasps inhabiting cooler areas show more spotted and broken facial patterns than those living in warmer areas (Tibbetts et al. 2011a, b; Green et al.

2012). Moreover, Green et al. (2012) experimentally showed that wasps reared during the pupal stage in cooler conditions had higher brokenness than their nestmates reared in warmer conditions. Basically, variation in melanin pattern can play a role for efficient thermoregulation in different thermal conditions, by permitting more rapid body heating (Green et al. 2012). But, as underlined by Tibbetts and Dale (2004), the amount of melanin on the clypeus represents less of 1 % of the total amount of the pigment on the body surface and it is not known if wasps with more black clypeus show also greater body melanisation, The abundance of wasps with entirely yellow clypeus in South Europe populations (Spain and Italy) may thus locally limit the evolution of visual social recognition (Green et al. 2012) thus explaining the contrasting results obtained by studies carried out on populations of different climatic areas.

A badge of status is expected to be a reliable signal of quality and its honesty (association between true quality and signaling) is maintained and enforced by social costs (Smith and Harper 2003). As expected, in the American population of *P. dominula* studied by Tibbetts and Dale (2004), all indicators of status badge (number of spots, percentage of clypeus pigmented black and brokenness index) were correlated with body size of foudresses (measured as head width) that is a good predictor of dominance (even if no absolute, see Cervo et al. 2008), suggesting that clypeus marks represent reliable indicator of quality. Moreover, facial brokenness was also found to be linked to titers of Juvenile Hormone, a hormone involved in agonistic a interactions (Tibbetts et al. 2011a, b). Support for the importance of facial pattern as quality signal comes also from the study of the signal developmental properties. While having an heritable component, the quality signal is highly influenced by environmental factors during larval and pupal life. In addition to the importance of temperature (Green et al. 2012), food supplementation experiments showed that rearing conditions influence quality signal development in American population (Tibbetts and Curtis 2007). Wasp larvae reared with supplemental food develop facial patterns advertising higher agonistic quality (i.e. higher brokeness) than larvae reared without supplement, supporting the idea that black marks convey information of quality linked to early nutrition. These findings could also account for the different facial pattern in *Polistes* "castes" (Tibbetts 2006a; Tibbetts et al. 2011b): workers, which experience reduced larval nutrition compared to foundresses (Toth et al. 2009), show lower facial pattern brokenness.

Other species of wasps showing variable clypeus pigmentation patterns have been tested to assess whether variable facial pattern function as a conventional signal of agonistic ability. Three species of *Polistes* paper wasps, *P. satan* (Tannure-Nascimento et al. 2008), *P. exclamans* (Tibbetts and Sheehan 2011), *P. gallicus* (Petrocelli et al. 2014) and a stenogastrine wasp, *Liostenogaster vechti* (Baracchi et al. 2013) showed visual markers that convey information on agonistic ability.

However, different studies have used different indicators of quality in addition to body size. Reproductive status (measured as ovarian development) was found to be linked to variation of visual signals both in the stenogastrine wasp *L. vechti* (Baracchi et al. 2013) and in *P. satan* (Tannure-Nascimento et al. 2008), being the wasps with more developed ovaries (i.e. dominant individuals) those with more dark facial markings.

Contrary to what was expected, nor correlation between facial pattern parameters and foudresses body size (and body weight), (Cervo et al. 2008; Zanette and Field 2009; Green et al. 2012), neither correlation between facial pattern and both probability of surviving winter and health status (Cervo et al. 2008) were found in European populations of the species, confirming that clypeus pattern doesn't mirror the true quality of bearer in wasps belonging to such populations (but see Tibbetts et al. 2011a, b for contrasting results).

Although all these studies provide correlational evidences for facial pattern as quality signal, a simple test to evaluate the assessment of conspecifics via visual clypeus markers during foraging contexts has furnished an experimental support for facial markers as quality signal in *P. dominula* (Tibbetts and Lindsay 2008). Wasps were tested in choice trials to evaluate their preference for food patches guarded by conspecifics with different facial pattern; they showed to perform their choice on the basis of the guard facial pattern by avoiding to eat food patches controlled by guards with facial patterns indicating a high quality level. Moreover, Tibbetts (2008) provided evidences that the tested wasp responses to guard badge are context dependent. However, when the test was repeated in a native European population (Spain, Green and Field 2011a) no evidences that wasps use facial pattern to assess rival quality were found, confirming again no communicative role of clypeus marks in European populations. More recently, another study (Branconi et al. in prep.), tested for a signal function of the clypeal pattern by presenting wasp lures with different facial patterns to colonies of another native population (Italy) and showed that clypeal patterns are not involved in rival assessment in a competitive context (colony defense).

Finally, facultative intraspecific parasitism—i.e. nest usurpation by a conspecific female- is another context (Cervo and Dani 1996; Cervo 2006) where information born on facial pattern could be used by colony owners to assess the fight ability of potential rivals. Tibbetts and Shorter (2009) showed that the outcome of the context in *P. dominula*—conflict *versus* cooperation—is influenced by both facial pattern an body size. Challenger with more facial markers than the nest owner has more probability to usurp the colony that challenger with fewer markers than owner. An analogous result has been found in the European species *Polistes gallicus* (Petrocelli et al. 2014): queens of this solitary founding species usually experience a high rate of intraspecific usurpation (Dani and Cervo 1992) and they use visual black mark on the clypeus of the potential usurper to assess the opponent fighting ability (Petrocelli et al. 2014) and modulate their response. Moreover, Tibbetts and Injaian (2013) found that foundresses of *P. dominula* preferentially associate with other foundresses that have similar facial pattern. This tendency may increase the likelihood to form associations among related individuals as wasps from the same nest have more similar facial patterns (Tibbetts 2006a, b; Tibbetts et al. 2010). As a result, co-foundresses associations in wild colonies could be influenced by facial pattern similarity (Tibbetts and Injaian 2013) in addition to the well-known role of chemical signature similarity (Dapporto et al. 2004), even if stable and free-conflict cooperation would be based on a differential facial pattern hierarchy (Tibbetts and Dale 2004).

Overall, the growing literature on this topic suggest facial pattern could work as badge of status in some populations (e.g. North America) but not in other (e.g. Spain and Italy). It is possible that these contrasting results could be partially due to the different parameters used to evaluate (i) the variation in facial pattern (the sheer number of spots, the percentage of black area on the clypeus or the more complex brokenness index), (ii) the individual quality (size, weigh, ovarian development, health status), and (iii) the measures of dominance in the different studies. For example, it could be important to confirm the goodness of plastic arena experiment carried out for two hours as generalization of what happens into the wild because, in nature, the establishment of the dominance hierarchy requires often long time and sometimes it can change with the time. Returning to the field to verify the results obtained in captivity is thus fundamental. For example, the comparison of quality signals between gynes (future foundresses) and queens (top rank foundresses) suggests that brokeness is indeed not strongly associated with reproductive success. As not all gynes will survive winter until the founding phase and become queens on their nest (as they may be subordinate foundresses of low social rank, not having reproductive benefits) we can predict successful queens to have higher quality signals than gynes. Contrarily, Tibbetts et al. (2011a, b), investigated several populations along a latitudinal gradient in Europe and North America and found that gynes and queens have similar facial patterns (Cervo et al. 2008; Tibbetts et al. 2011a, b). As a confirmation, the only studies carried out so far on *Polistes* to evaluate the importance of facial patterns in wild population failed to find any adaptive value associated with facial patterns (Cervo et al. 2008; Green and Field 2011a). A similar investigation in the American population will reveal the importance that facial patterns play in *P. dominula* in the wild and it is thus strongly needed to conclusively evaluate the importance of facial patterns in the population where most positive evidence have been collected (Green and Field 2011a).

Individual and Familiar Recognition

The most accurate form of social recognition is IR, i.e. the ability to recognize individuals according to their distinctive features (Halpin 1980, Dale et al. 2001, Wiley 2013). This ability can convey relevant benefits to social animals, both in competitive and cooperative interactions. Whenever there are repeated interactions among multiple individuals with differing features and states, IR may allow to modulate social behaviour according to prior experience with specific individuals. For example, when scrambling for a limited resource, opponents may benefit by avoiding repetition of costly fights by individually recognizing specific high quality opponents (Tibbetts and Dale 2007). Thanks to its benefits (despite some costs, in particular the lower possibility to cheat when having easily recognizable distinctiveness, see Tibbetts and Dale 2007) IR recognition is now considered to be widespread both in vertebrates and invertebrates (reviewed in Gherardi et al. 2012 for invertebrates, Halpin 1980 and Tibbetts and Dale 2007 for vertebrates).

Insect societies are not usually considered as harbouring IR abilities, being thus often represented as impersonal societies lacking specific individual bonds (Wilson 1971). Indeed, the usually large size of the colony and the short life of its members may prevent the evolution of IR and promote, on the contrary, other kind of social recognition such as familiar and nestmate recognition. Not all insect societies however reach the highest peaks of complexity and crowdedness. In many genera of primitively eusocial species, such as Polistinae and Stenogastrinae, societies are formed, for a large (or even the entire) part of their colony cycle, by just few to dozens individuals (Reeve 1991; Turillazzi 2012). These societies are usually characterized by intense direct conflict over access to reproduction, which are regulated by complex yet stable social interactions (Bourke 1999). Being able to recognizing who's who and behave appropriately may thus reveal to be crucial.

Recently, a case of IR have been suggested (Tibbetts 2002) to exists in a temperate paper wasp species from North America, *Polistes fuscatus*, which has some crucial features that qualifies it as potentially harbouring IR: (1) small group size and (2) repeated social interactions that (3) dramatically affect individual fitness payoffs among (4) individuals with highly variable distinctiveness.

Similarly to *P. dominula, P. fuscatus* colonies are usually founded by multiple foundresses in Spring and a linear hierarchy is soon established. *P. fuscatus* females have a very large phenotypic variability in their yellow facial and abdominal markings, which may be present or absent and vary in width and length (Fig. 8.1, Tibbetts 2002).

Tibbetts (2002) demonstrated that the presence of these markings allow wasps to recognize individuals with which they previously interacted (e.g. nestmates). When a wasp was returned to the nest after an experimental manipulation of her facial or abdominal markings with paint, she received more aggressions from nestmates than a control wasp (painted in a way that did not alter their markings) (Tibbetts 2002). As predicted for actual identity signals (Dale et al. 2001), *P. fuscatus* facial and abdominal markings are not condition dependent as they are not associated with wasp size or dominance rank, (Tibbetts 2002) nor with wasp pre-emergence rearing conditions (Tibbetts and Curtis 2007).

This recognition ability is achieved learning the yellow-black patterns of the wasp, as proved by the fact that aggression toward nestmates with altered markings declines over time, as these novel marking configuration becomes familiar to nestmates (Tibbetts 2002). Indeed, *Polistes fuscatus* wasps seem to be specialized in face learning. Through a conditioning protocol Sheehan and Tibbetts (2011) were able to show that *P. fuscatus* are more skilled at learning to recognize wasp faces than non face images or manipulated faces (such as re-arranged or antennae-less faces).

The markings configuration learned in social encounters is then stored in wasp brain and wasps are able to retain this information up to one week after, even if multiple social interactions with many other wasps occur during this period (Sheehan and Tibbetts 2008). Such long term memory may be stabilized via protein synthesis, as occur in long term olfactory memory in ants (Guerrieri et al. 2011).

The experiment discussed above showed that female *P. fuscatus* use facial and abdominal markings to recognize individuals with whom they have previously interacted or seen. According to Tibbetts and Dale (2007) this ability can be classified as IR and, indeed, the same experimental approach has been used to assign IR abilities in many species of invertebrates and vertebrates (Tibbetts and Dale 2007; Gherardi et al. 2012). However, disentangling IR from other form of class level recognition (such as familiar recognition) is not an easy task (Tibbetts and Dale 2007; Gherardi et al. 2012; Wiley 2013). Indeed, the IR definition itself has been debated (Tibbetts and Dale 2007; Steiger and Muller 2008; Tibbetts et al. 2008) and the extent to which invertebrate species are able of IR still remain uncertain (Thom and Hurst 2000; Gherardi et al. 2012; Wiley 2013). A key feature of IR process is that it requires individuals to "uniquely identify each social partner" (Becher 1989; Lai et al. 2005; Tibbetts and Dale 2007), i.e. each individual should be treated in a specific way according to the significance it has to the subject. The largest part of studies on IR has unfortunately the shortcoming of not allowing to separate familiar recognition from true IR (Lai et al. 2005; Gherardi et al. 2012; Wiley 2013). Indeed, the first occurs when individuals discriminate between familiar and unfamiliar conspecifics, i.e. previously met or not met individuals, by showing for example reduced aggression or reduced interest in known partners. This recognition is indeed a class-level recognition, in which individuals are categorized in two classes (met or not previously met, unknown) and it is very widespread in invertebrates (Gherardi et al. 2012). True individual recognition (TIR) is, on the contrary, the ability to discriminate among individuals, who may share several features (such as familiarity, dominance rank, gender), on the basis of a specific configuration of their features (e.g. appearance, odour, behaviour), (Gherardi et al. 2012; Wiley 2013). From an operational point of view it should be tested by evaluating if individuals show different responses to equally familiar individuals with differing significance to the subject (Lai et al. 2005). Currently, no specific experiments to test this possibility have been undertaken in social wasps (Wiley 2013). The most parsimonious hypothesis is thus that social wasps show familiar recognition thanks to the use of visual cues.

The ability to perform familiar recognition on the basis of visual cues could be indeed quite widespread in social wasps. As far as there is enough variability in markings to allow for distinctiveness among a certain number of frequently encountered partners (such as nestmates in small insect societies) and the rest of unknown/unfamiliar conspecific individuals (which seems to be the case for many *Polistes* and stenogastrine wasps), the ability to learn specific configuration of facial/abdominal marking should not be out of the possibility of social wasps. Indeed, the finding that familiar recognition based on visual cues also occurs in a hover wasp (*L. flavolineata*, Baracchi et al. 2013) suggests the intriguing hypothesis that this ability may be quite common in social wasps.

Visual Recognition and Sex

Generally, in Hymenoptera, male-male competition for mate and mate choice occur far from the nest. In such a context, an information exchange between male and female is required to recognize species, sex, sexual maturity and to attract and find each other. In social wasps, males typically have lek- or swarm-based mating systems (see Turillazzi and Cervo 1982; Beani et al.1992; Beani 1996; Turillazzi 2012; Batra 1980; Spiewok et al. 2006). Males typically patrol non resource sites at species-specific time of the season and/or hours of the day. Male performances usually occur at traditional landmarks that differ for location among sympatric species. Conspicuous aggregation of mature males at species-specific timing and landmarks visually attract conspecific females facilitating successful outbreeding.

However, male fitness is limited by the availability of females visiting males aggregations and males vigorously compete at leks or at swarms to gain access to females. On the other hand females have a wide choice of males and gain in fitness by recognizing high quality males. This results in skewing reproduction among males and in selecting male ornaments to minimize competition costs and address female choice (Andersson and Simmons 2006).

Males of some species of social wasps are reported to use visual signals that allow recognition of strength ability during intra-sexual conspecific competition and, at the same time, of male quality to address the female choice.

Males of several species of stenogastrine wasps exhibit a visual display during their patrolling behavior in shady wet tropical forest (for a review see Turillazzi 2012). During their aerial displays, males of *Parischnogaster* wasps, by extending their abdomens, show large white stripes on the dorsal anterior part of the gasters that are conspicuous visual spots against the dark background of the forest. These strips become invisible when males don't stretch their abdomen during patrolling flights or are in resting position. Moreover, the white stripes are a sexual dimorphic trait as they lack in females. These stripes described for the first time by Padgen (1962) for *Metischnogaster cilipennis*, *M. drewseni* and *Parishnogaster striatula*, have been reported more recently for other species, such as *Parishnogaster mellyi* and *P. nigricans serrei* (Turillazzi 2012). Male of *P. mellyi* usually perform a zig-zag display after the prolonged stripes display (Beani and Turillazzi 1994). The duration and the frequency of this performance are positively correlated both with the outcome of aerial duels and the permanence on the patrolling spots until the arrival of the females which occurs towards the end of the patrolling period; this suggests that this male trait may give information to recognize both male strength and quality (Beani and Turillazzi 1999). Experimental manipulation of white stripes in a captivity study on *P. mellyi* males (Beani and Turillazzi 1999) demonstrated the function of this visual ornament as badge of status (Berglund et al. 1996): the addition of one white stripe on the abdomen of male elicits more inspections/aggressions by competitors and more explorations by flying females (Beani and Turillazzi 1999). Interesting, artificially white-painted males showed to be unable to support the social cost induced by the alteration of their badges: they shortened the period and the frequency of their visual display and performed very frequently feeding stops during their performance. This suggests that the visual white-stripes exhibition has costs for the patrolling males and only individuals of good quality resist at prolonged visual display.

Analogously, two recent papers on *P. dominula* (Izzo and Tibbetts 2012) and *P. simillimus* (De Souza et al. 2014) suggested that sexually selected visual signals could be important in males of *Polistes* paper wasps too. In *P. dominula* visual signals of males may be represented by dorsal yellow spots placed on the first abdominal segment. Similar spots are present on females too but they lack the variation which characterizes males dorsal spots. According to Izzo and Tibbetts (2012), the sexually dimorphism and the variation in both size and shape of male dorsal spots make them excellent candidates as recognition signals in both intra- and intersexual selection. In *Polistes* wasps, males aggregate at traditional landmarks (Beani and Turillazzi 1988; Beani et al. 1992; Beani 1996), where each male vigorously defends little territory against other males. This lek-based mating system allows females to make their mating choices by sporadically visiting such areas where males gather and maintain their leks. Laboratory experiments carried out by Izzo and Tibbetts (2012) showed that *P. dominula* males with smaller and elliptically shaped spots were more dominant over other males, were often the winners during the male-male contests and were more preferred by females. Once again manipulation of male spots shape and size showed that the morphology of yellow spots works as quality signal driving the outcome of both intra- and inter-sexual interactions. According to Izzo and Tibbetts (2012) an unexpected data regards the lack of relationships between male dominance and female choice as generally it is assumed that female preference is based on male rank position, suggesting that in this species female choice probably is not simply based on male rank (Izzo and Tibbetts 2012). Similar to *P. dominula*, also *P. simillimus* show sexual dimorphism and variation in size and shape of male head pigmentation and abdominal spots, both of which seem to influence females mating choice (De Souza et al. 2014). However, it should be considered that male dominance data were obtained in both cases in artificial context very different from what happens in the wild (and indeed, for *P. simillimus*, male behavior in the field is not known, De Souza et al. 2014). In the field, *P. dominula* males defend their territories by engaging very strong competitions with neighboring males but no dominance contexts (with bites, mounts and submissive behavior) are observed (Beani 1996). It is possible that other parameters of male performance not obviously considered in a laboratory study (such as territory size and its localization in the lekking area or/and the male flight activity at the lek) may be the basis of *P. dominula* female choice. Although the laboratory results on visual ornaments of *P. dominula* and *P. simillimus* males are intriguing, future studies carried out in the wild will be fundamental to better understand the role of visual recognition signals at leks, as pointed out by Izzo and Tibbetts (2012).

Visual Signalling Between Species

The researches discussed so far suggested that visual cues play a relevant role in social recognition between conspecific individuals, in particular shaping intraspecific aggressive interactions. Conflicts, however, may also occur among species and competition between sympatric species may be associated with the access to limited resources such as food or nesting sites (e.g. *P. dominula* and *P. nimpha* in southern Europe, Lorenzi and Caprio 2000, or *P. dominula* and *P. fuscatus* in North America, Gamboa et al. 2002), and with nest usurpation (Cervo and Dani 1996; Cervo et al. 2004; Cervo 2006).

The large variability in *Polistes* facial markings (at both the intra and interspecific level), together with their use in intraspecific communication in several species, opens the possibility that visual cues play a role also in interactions between species.

An outstanding model to evaluate the importance of visual signalling in interspecific contests is represented by *Polistes* social parasites and their hosts. Social parasites exploit the host parental cares in order to rear their own brood, saving the costs of building the nest, foraging and taking caring of the brood (Wilson 1971). Inside *Polistes*, obligate social parasitism—i.e. species lacking the worker caste and unable to found colonies on their own—occurs in three monophyletic species: *Polistes sulcifer*, *P. semenowi* and *P. atrimandibularis* (Cervo and Dani 1996; Cervo 2006; Choudary et al. 1994; but see Buck et al. 2012 for the possible existence of other parasitic species in north America). Parasitism is the only reproductive option for *Polistes* obligate social parasites as they must completely rely on the host worker brood care to rear their own reproductives (Cervo 2006). Parasitism imposes dramatic costs to the host colony, which usually is not able to produce reproductives (Cervo 2006, but see Cini et al. 2014 for evidence of workers rebellion).

The diametrically opposed interests of social parasites and hosts, represented strong selective pressures that led to the evolution of several morphological, physiological and behavioural adaptations in both species (Cervo 1994, 2006; Lorenzi 2006; Ortolani et al. 2008; Ortolani and Cervo 2009, 2010; Petrocelli and Turillazzi 2013). In particular, social parasites evolved sophisticated sensory deception mechanisms to break host's barriers by exploiting their communication systems (Lorenzi 2006). At the same time, hosts may benefit from developing their recognition system and tuning their visual abilities toward the recognition of parasites and the assessment of their strength.

Visual cues could be involved in host-parasite interactions in two main ways. On one hand, hosts may be selected to recognize the "possible" differences in parasite appearance to readily recognize parasites and adopt the best possible strategies to counteract them. On the other hand, parasites may be selected to exploit host visual recognition system to deceive the host. As far as the host recognition system depends on visual cues, it would be advantageous for the parasite to evolve specific adaptations to visually trick the host.

Recently, a possible case of the involvement of visual cues in between-species interaction has been suggested to exist in the social parasite–host system *P. sulcifer–P. dominula*. *P. sulcifer* has conspicuous black patterning on the clypeus, which consists in a black band which is usually contiguous to the black mandibles, forming a continuous large black area in the lower part of the face (Ortolani et al. 2010), (Fig. 8.1). Behavioural bioassays with lures presentation (heads of dead wasps with different facial patterns) showed that the peculiar parasite facial pattern reduces host aggressiveness: host foundresses were more aggressive toward conspecific heads than toward parasite heads (Ortolani et al. 2010). Experimental pattern manipulation revealed in addition that the black lower part of the parasite clypeus (hereafter band) is the trait responsible for this reduction in aggressive responses, as parasites with artificially removed black band were more attacked than control parasites (Ortolani et al. 2010).

The first, most logical explanation is that parasites reduce host aggressiveness as their facial pattern signals a high status and good fighting abilities. This could occur by ‘tricking’ host foundresses by using host signalling system.

As discussed above, clypeal patterns in the host species are suggested to function as status signals (or ‘badges’) that indicate the resource holding potential of the bearer (Tibbetts and Dale 2004), so that foundresses modulate their aggressiveness toward unfamiliar opponents on the basis of their visual appearance (Tibbetts and Dale 2004; Tibbetts and Lindsay 2008; Tibbetts et al. 2010). The clypeal patterns of the parasite may thus similarly function as signals of status, conveying the information of a high quality and highly dangerous bearer, finally decreasing host foundress’s aggressiveness (Ortolani et al. 2010, Green and Field 2011b for *P. semenowi*). Alternatively, parasites may have evolved an independent quality signaling system, in which different facial pattern honestly mirror individual quality (e.g. fighting ability), and host foundress may thus evaluate opponents fighting abilities upon their facial patterns. Some considerations seem however to argument against both hypotheses. First, the link between opponents facial patterns and aggressive responses has not been confirmed in the native range of *P. dominula*, where parasite-host interaction takes place (Green and Field 2011b; Branconi et al. in prep). Moreover, the parasite pattern is not exactly the same as the host one: the black area is relevantly larger, it extends down to the mandibles and melanin is more uniformly distributed across the clypeus, thus largely reducing pattern disruption (Ortolani et al. 2010; Green and Field 2011b). Finally, parasite facial pattern is not related to any fighting ability parameter taken into account so far (Cini et al. 2015).

An alternative hypothesis is that the reduction in host aggressiveness toward parasites may occur because the black band amplifies the width of the mandibles, which represent the primary weapon used during fight between *Polistes* wasps (Cervo 2006). Indeed, in the host species, mandibles are black and surrounded by yellow facial areas, so that host foundresses may estimate mandibular size of the opponents (and thus their fighting ability) by evaluating the size of the black area in the lower part of the head. When faced to a parasite head, foundresses would overestimate its mandibular size, thus reducing their aggressiveness to avoid fatal injuries (Ortolani et al. 2010). Ortolani et al. (2010) considered the black band attached to the mandibles as a signal that visually amplifies the mandibular width, thus giving information about the parasite's dangerousness.

This hypothesis did not receive support from recent experiments (Cini et al. 2015). A key assumption is that parasites may benefit from amplifying their mandibular size only if hosts use this cue during intraspecific encounters, that is to say if host aggression toward conspecific intruders depends, among many factors, also on their mandibular size. However, no difference was observed in the aggressive response of *P. dominula* foundresses toward conspecific head lures with mandibles size artificially manipulated with paint (increased or decreased) suggesting that the host species females do not rely on opponents mandible size to modulate their aggression (Cini et al. 2015). This makes rather unlikely that parasites evolved a visual cheating strategy based on the amplification of a cue not taken into account by the host they must cheat.

The likelihood that facial pattern evolved as sensory deception strategy by the parasite is also made less likely by the null fitness benefits associated to a particular clypeal patterning (Cini et al. 2011; Green and Field 2011b). Laboratory studies which used real usurpation demonstrated that clypeal patterning has a null role in determining the outcome of usurpation contests: parasites with different facial patterns had no different chances of winning a contest with the host (Cini et al. 2011; Green and Field 2011b). On the contrary, head size was the only determinant predictor of the likelihood of winning an usurpation contest (Cini et al. 2011; Green and Field 2011b).

Turning the attention to the host ecology may help to find an explanation. While parasitisation represents a very dangerous event for *P. dominula*, also conspecific individuals represent a major threat. Indeed, nest usurpation by foundresses from other nests is very common in this species, likely due to nest failure or predation (Cervo unpublished data). Despite obligate parasite prevalence could be locally very high (up to 50 % of nests are parasitized in some populations, Ortolani and Cervo 2010), the largest part of *P. dominula* populations experience a null or low parasitic pressure, as parasites are restricted to host populations near mountains, were parasites overwinter (Cervo 2006). Moreover, we could expect intraspecific parasitism pressure to be even higher in parasitized populations, where foundresses displaced by the parasites will try to usurp other conspecific nests. Overall, we may suppose that intraspecific parasitism could be a more common threat for *P. dominula* foundresses. So, a possibility to explain the lower aggressiveness toward parasites head is thus that for *P. dominula* foundresses a conspecific intruder may represent a bigger threat than a parasite. Consequently, host foundresses would thus react more aggressively toward conspecific intruders than parasites. Indeed, lure presentation experiments showed that when the parasite facial pattern is altered by displacing the black band in the middle of the clypeus, thus mimicking a host-like facial pattern, host aggression increases (Cini et al. 2015).

Evolution of Visual Recognition Abilities and Conclusive Remarks

The main pressures that shape social life selected for the evolution of a full range of recognition systems in primitive insect societies. The paradigm that social insects live in a world of smell and that their social life is governed by chemicals has probably hidden the importance of other communication channels in social recognition. In particular, the possible influence of visual cues remained rather under estimated for many decades but the last 10–15 years saw an increasing attention toward the visual channel with various theoretical and experimental researches, especially in *Polistes* and stenogastrine wasps. Despite only few social wasp species have been investigated for the use of visual cues in some types of social recognition, almost all showed this ability, suggesting that this ability could be widely widespread in social wasps.

The independent evolution of this ability in Stenogastrinae and *Polistes* and the use of these cues for different purposes in different species (e.g. familiar recognition or badge of status) suggest moreover that social and ecological pressure might easily overcome physiological/phylogenetic constraints, allowing social wasps to rapidly evolve specific social recognition systems based on visual cues.

From an evolutionary point of view, the likelihood of evolving this recognition ability will be favoured by low constraints (e.g. physiological, such as low signal production costs and low complexity of the required perceptual ability) and by a high selective pressure (i.e. high benefits associated with the presence and use of visual cues). Despite the very limited knowledge about the signal production and perception mechanisms, some evidences suggest that both production and perception of visual signals (body markers) would be not so costly in social wasps. While the influences of nutritional and climatic factors seem to be important for the development of the signal, its production seems quite cheap for the individual and different patterns seem to have low differential production costs (Tibbetts and Dale 2004).

Regarding visual signal perception, despite a limited knowledge of the process, it seems evident that particular well developed recognition abilities are not required. Mini brain of insects are well equipped to visual cognitive task (Avargues-Weber et al. 2011) and analyses of neuronal networks showed that even complex tasks, such as face recognition, can be achieved with only a few hundreds neurons (Aitkenhead and McDonald 2003). Moreover, neuroanatomical analyses showed that, despite the possible presence of some neural specialization in species showing visual recognition abilities, paper wasps might be preadapted for visual pattern discrimination (Gronenberg et al. 2008). It is indeed likely that neural circuitry similar to that used by insects for prey recognition and navigation was fairly sufficient also for social recognition and was co-opted (and maybe only slighty re-wired) by those social insects species experiencing pertinent selection pressures (Gronenberg et al. 2008; Chittka and Dyer 2012). The ability of using visual cues to recognize social partners should not surprise. Indeed, social insects seem to have a quite good visual acuity, and “minibrains” of Hymenoptera have been shown to be keen on many visual tasks, from simple to complex ones (Avargues-Weber et al. 2011). Recent evidence moreover suggests that visual perception may have specifically coevolved with visual signalling in *Polistes* genus (Sheehan et al. 2014)

Despite much attention has been paid to propose and discuss possible selective pressures favouring the evolution of different types of visual recognition in social wasps (discussed in previous sections), reliable estimation of fitness benefits associated with visual recognition in different species and contexts has not been performed for most of the recognition types. For example, facial patterns in *P. dominula* have been shown to be not linked to any adaptive value in the wild (Green and Field Green et al. 2013). So far, the link between facial pattern and fitness benefits has been proved only in *P. fuscatus*, where wasps with variable faces that allow recognition receive less aggression than wasps which have with common indistinguishable faces (Sheehan and Tibbetts 2009). Future studies should focus on proximate and ultimate factors to reveal mechanisms, benefits and costs of visual recognition systems that may have triggered their evolution (Chapuisat 2004). While our knowledge on the matter is now increased, we are quite far from having a complete and clear picture and, as shown in the corresponding sections on this review, both visual signalling of badge of status and visual IR still deserve attention and further experimental approaches to understand the underlying processes and their evolutionary importance (Green et al. 2013; Gherardi et al. 2012; Chapuisat 2004; Wiley 2013). A major target of future researches should be to understand how visual cues interact with cues from other sensory channels, especially chemical ones (e.g. Boyle and Tricas 2014). It is possible that *Polistes* wasps can use chemicals or visual cues in different situations/contexts. Cuticular hydrocarbons blend and visual facial markers are contemporaneously bear by individual wasps so it is not easy to evaluate when and in which context chemicals or visual signals are used to convey the necessary information. At the moment, very few studies have been carried out (but see Ortolani et al. 2010; Cappa 2012; Baracchi et al. 2015) to evaluate the relative importance of a communicative channel over the other in a given context. Experiments to decouple visual and chemical signals should be necessary for completely understanding the communication system in primitively wasps. On the other hand, as chemical communication play an overwhelming importance in social insect life, a key aspect would be to understand whether chemical and visual stimuli interact in allowing specific type of recognition (e.g. familiar, individual, quality), and eventually how they contribute to build multimodal signals.

Acknowledgments We are grateful to D. Baracchi, F.S. Nascimento and E.A. Tibbetts for providing photos of wasp faces to be published. We would like to thank Elizabeth A.Tibbetts for her insightful and helpful comments on the manuscript. Funding was provided by the University of Florence (to RC and ST) and the Foundation Fyssen (to AC).

References

Aitkenhead M, McDonald AJS (2003) A neural network face recognition system. Artif Intell 16:167–176

Andersson M, Simmons LW (2006) Sexual selection and mate choice. Trends Ecol Evol 21:296–302

Avarguès-Weber A, Deisig N, Giurfa M (2011) Visual cognition in social insects. Annu Rev Entomol 56:423–443

Baracchi D, Petrocelli I, Cusseau G, Pizzocaro L, Teseo S, Turillazzi S (2013) Facial markings in the hover wasps: quality signals and familiar recognition cues in two species of Stenogastrinae. Anim Behav 85:203–212

Baracchi D, Petrocelli I, Chittka L, Ricciardi G, Turillazzi S (2015) Speed and accuracy in nest-mate recognition: an hover wasp prioritizes face recognition over colony odour cues to minimize intrusion by outsiders. Proc R Soc B 282 (1802): 20142750 doi:10.1098/rspb.2014.2750

Batra SWT (1980) Sexual behaviour and pheromones of the European hornet, *Vespa crabro* germana (Hymenoptera: Vespidae). J Kansas Entomol Soc 53:461–469

Beani L (1996) Leklike courtship in paper wasps: "A prolonged, delicate, and troublesome affair". In: Turillazzi S, West-Eberhard MJ (eds) The natural history and evolution of paper-wasps. Oxford University Press, Oxford, pp 113–125

Beani L, Turillazzi S (1988) Alternative mating tactics in males of *Polistes dominulus* (Hymenoptera: Vespidae). Behav Ecol Sociobiol 22:257–264

Beani L, Turillazzi S (1994) Aerial patrolling and stripes display in males of *Parischnogaster mellyi* (Hymenoptera Stenogastrinae). Ethol Ecol Evol Spec Issue 3:43–46

Beani L, Turillazzi S (1999) Stripes display in hover-wasps (Vespidae: Stenogastrinae): a socially costly status badge. Anim Behav 57:1233–1239

Beani L, Cervo R, Lorenzi MC, Turillazzi S (1992) Landmark-based mating systems in four *Polistes* species (Hymenoptera, Vespidae). J Kansas Entomol Soc 65:211–217

Beecher MD (1989) Signalling systems for individual recognition: an information theory approach. Anim Behav 38:248–261

Berglund A, Bisazza A, Pilastro A (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. Biol J Linn Soc 58:385–399

Bourke AFG (1999) Colony size, social complexity and reproductive conflict in social insects. J Evol Biol 12(2):245–257

Boyle KS, Tricas TC (2014) Discrimination of mates and intruders: visual and olfactory cues for a monogamous territorial coral reef butterflyfish. Anim Behav 92:33–43

Buck M, Cobb TP, Stahlhut JK, Hanner RH (2012) Unravelling cryptic species diversity in eastern Nearctic paper wasps, *Polistes (Fuscopolistes)*, using male genitalia, morphometrics and DNA barcoding, with descriptions of two new species (Hymenoptera: Vespidae). Zootaxa 3502:1–48

Cappa F (2012) The male phenotype in *Polistes dominula*: sexual selection and host-parasite interactions. PhD thesis, University of Florence

Cervo R (1994) Morphological adaptations to the parasitic life in *Polistes sulcifer* and *P. atrimandibularis* (Hymenoptera Vespidae). Ethol Ecol Evol 6:61–66

Cervo R (2006) *Polistes* wasps and their social parasites: an overview. Ann Zool Fenn 43:531–549

Cervo R, Dani FR (1996) Social parasitism and its evolution in *Polistes*. In: Turillazzi S, West-Eberhard MJ (eds) The natural history and evolution of paper-wasps. Oxford University Press, Oxford, pp 98–112

Cervo R, Zacchi F, Turillazzi S (2000) *Polistes dominulus* (Hymenoptera, Vespidae) invading North America: some hypothesis for its rapid spread. Insectes Soc 47:155–157

Cervo R, Stemmer C, Castle W, Queller D, Strassmann JE (2004) Social parasitism of *Polistes dominulus* by *Polistes nimphus* (Hymenoptera, Vespidae). Insectes Soc 51(2):101–108

Cervo R, Dapporto L, Beani L, Strassmann JE, Turillazzi S (2008) On status badges and quality signals in *Polistes dominulus*: body size, facial colour patterns and hierarchical rank. Proc R Soc London B 275:1189–1196

Chapuisat M (2004) Evolution: social selection for eccentricity. Curr Biol 14:R1003–R1004

Chittka L, Dyer A (2012) Your face looks familiar. Nature 481:154–155

Choudary M, Strassmann JE, Queller DC, Turillazzi S, Cervo R (1994) Social parasites in Polistine wasps are monophyletic: implications for sympatric speciations. Proc R Soc London B 257:31–35

Cini A, Bruschini C, Poggi L, Cervo R (2011) Fight or fool? Physical strength, instead of sensory deception, matters in host nest invasion by a wasp social parasite. Anim Behav 81(6):1139–1145

Cini A, Nieri R, Dapporto L, Monnin T, Cervo R (2014) Almost royal: incomplete suppression of host workers ovarian development b a social parasite wasp. Behav Ecol Sociobiol 68(3): 467–475. doi:10.1007/s00265-013-1661-z

Cini A, Ortolani I, Zechini L, Cervo R (2015) Facial markings in the social cuckoo wasp *Polistes sulcifer*: no support for the visual deception and the assessment hypotheses. Behav Process 111:19–24. doi:10.1016/j.beproc.2014.11.010

Dale J, Lank DB, Reeve HK (2001) Signaling individual identity versus quality: a model and case studies with ruffs, queleas, and house finches. Am Nat 158:75–86

Dani FR, Cervo R (1992) Reproductive strategies following nest loss in *Polistes gallicus* (Hymenoptera, Vespidae). Ethol Ecol Evol Spec Issue 2:49–53

Dapporto L, Pansolli C, Turillazzi S (2004) Hibernation clustering and its consequences for associative nest foundation in *Polistes dominulus* (Hymenoptera Vespidae). Behav Ecol Sociobiol 56(4):315–321

de Souza AR, Júnior CAM, do Nascimento FS, Lino-Neto J (2014) Sexy faces in a male paper wasp. PLoS One 9(5):e98172

Gamboa GJ, Greig EI, Thom MC (2002) The comparative biology of two sympatric paper wasps, the native *Polistes fuscatus* and the invasive *Polistes dominulus* (Hymenoptera, Vespidae). Insectes Soc 49(1):45–49

Gherardi F, Aquiloni L, Tricarico E (2012) Revisiting social recognition systems in invertebrates. Anim Cogn 15(5):745–762

Green JP, Field J (2011a) Interpopulation variation in status signalling in the paper wasp *Polistes dominulus*. Anim Behav 81:205–209

Green JP, Field J (2011b) Assessment between species: information gathering in usurpation contests between a paper wasp and its social parasite. Anim Behav 81(6):1263–1269

Green JP, Rose C, Field J (2012) The role of climatic factors in the expression of an intrasexual signal in the paper wasp *Polistes dominulus*. Ethology 118(8):766–774

Green JP, Leadbeater E, Carruthers JM, Rosser NS, Lucas ER, Field J (2013) Clypeal patterning in the paper wasp *Polistes dominulus*: no evidence of adaptive value in the wild. Behav Ecol 24(3):623–633

Gronenberg W, Ash LE, Tibbetts EA (2008) Correlation between facial pattern recognition and brain composition in paper wasps. Brain Behav Evol 71:1–14

Guerrieri FJ, d'Ettorre P, Devaud JM, Giurfa M (2011) Long-term olfactory memories are stabilised via protein synthesis in *Camponotus fellah* ants. J Exp Biol 214:3300–3304

Halpin ZT (1980) Individual odors and individual recognition: review and commentary. Biol Behav 5:233–248

Howard RW, Blomquist GJ (2005) Ecological, behavioral, and biochemical aspects of insect hydrocarbons. Annu Rev Entomol 50:371–393

Hunt JH, Richard FJ (2013) Intracolony vibroacoustic communication in social insects. Insectes Soc 60(4):403–417

Izzo AS, Tibbetts EA (2012) Spotting the top male: sexually selected signals in male *Polistes dominulus* wasps. Anim Behav 83:839–845

Kirchner WH (1997) Acoustical communication in social insects. In: *Orientation and communication in Arthropods*. Birkhäuser Basel, Switzerland, pp 273–300

Lai WS, Ramiro LLR, Helena AY, Johnston RE (2005) Recognition of familiar individuals in golden hamsters: a new method and functional neuroanatomy. J Neurosci 25(49):11239–11247

Liebert AE, Gamboa GJ, Stamp NE, Curtis TR, Monnet KM, Turillazzi S, Starks PT (2006) Genetics, behavior and ecology of a paper wasp invasion: *Polistes dominulus* in North America. Ann Zool Fenn 43:595–624

Lorenzi MC (2006) The result of an arms race: the chemical strategies of *Polistes* social parasites. Ann Zool Fenn 43:550–563

Lorenzi MC, Caprio P (2000) Nest recognition in neighboring colonies: a comparison of two European species of *Polistes* wasps (*P. dominulus* and *P. nimphus*, Hymenoptera: Vespidae). J Ethol 18(2):65–68

Nieh JC (2004) Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini). Apidologie 35:159–182

Ortolani I, Cervo R (2009) Coevolution of daily activity timing in a host–parasite system. Biol J Linn Soc 96(2):399–405

Ortolani I, Cervo R (2010) Intra-specific body size variation in *Polistes* paper wasps as a response to social parasite pressure. Ecol Entomol 35(3):352–359

Ortolani I, Turillazzi S, Cervo R (2008) Spring usurpation restlessness: a wasp social parasite adapts its seasonal activity to the host cycle. Ethology 114(8):782–788

Ortolani I, Zecchini L, Turillazzi S, Cervo R (2010) Recognition of a paper wasp social parasite by its host: evidence for a visual signal reducing host aggressiveness. Anim Behav 80:683–688

Pagden HT (1962) More about Stenogaster. Malayan Nat J 16:95–102

Pardi L (1948) Dominance order in *Polistes* wasps. Physiol Zool 21:1–13

Petrocelli I, Turillazzi S (2013) Comparative morphology of Van der Vecht's organ in *Polistes* social parasites: host ecology and adaptation of the parasite. Biol J Linn Soc 109(2):313–319

Petrocelli I, Ricciardi G, Rodrigues de Souza A, Ermanni A, Ninu A, Turillazzi S (2014) Visual signals of individual quality in a European solitary founding paper wasp. Ethology 121(3): 300–307. doi:10.1111/eth.12339

Queller DC, Zacchi F, Cervo R, Turillazzi S, Henshaw MT, Santorelli LA, Strassmann JE (2000) Unrelated helpers in a social insect. Nature 405:784–787

Reeve HK (1991) *Polistes*. In: Ross KG, Matthews RW (eds) The social biology of wasps. Ithaca, Comstock, pp 99–148

Rohwer S (1975) The social significance of avian winter plumage variability. Evolution 29:593–610

Rohwer S (1977) Status signalling in Harris' sparrows. Behaviour 61:107–129

Roper T (1986) Badges of status in avian societies. New Sci 109:38–40

Senar JC, Camerino M (1998) Status signalling and the ability to recognize dominants: an experiment with siskins (*Carduelis spinus*). Proc R Soc London B 265:1515–1520

Sheehan MJ, Tibbetts EA (2008) Robust long-term social memories in a paper wasp. Curr Biol 18(18):R851–R852

Sheehan MJ, Tibbetts EA (2009) Evolution of identity signals: frequency dependent benefits of distinctive phenotypes used for individual recognition. Evolution 63(12):3106–3113

Sheehan MJ, Tibbetts EA (2011) Specialized face learning is associated with individual recognition in paper wasps. Science 334(6060):1272–1275

Sheehan MJ, Jinn J, Tibbetts EA (2014) Coevolution of visual signals and eye morphology in *Polistes* paper wasps. Biol Lett 10(4):20140254

Smith JM, Harper DGC (1988) The evolution of aggression: can selection generate variability? Philos Trans R Soc B 319:557–570

Smith JM, Harper D (2003) Animal signals. Oxford University Press, Oxford

Spiewok S, Schmolz E, Ruther J (2006) Mating system of the European hornet *Vespa crabro*: male seeking strategies and evidence for the involvement of a sex pheromone. J Chem Ecol 32:2777–2788

Starks PT, Turillazzi S, West-Eberhard MJ (2006) *Polistes* paper wasps: emergence of a model genus. Ann Zool Fenn 43(5–6):385–386

Steiger S, Müller JK (2008) 'True'and 'untrue'individual recognition: suggestion of a less restrictive definition. Trends Ecol Evol 23(7):355

Strassmann JE (2004) Animal behaviour: rank crime and punishment. Nature 432(7014):160–162

Tannure-Nascimento IC, Nascimento FS, Zucchi R (2008) The look of royalty: visual and odour signals of reproductive status in a paper wasp. Proc R Soc London B 275:2555–2561

Thom MD, Hurst JL (2000) Individual recognition by scent. Ann Zool Fenn 41:765–787

Tibbetts EA (2002) Visual signals of individual identity in the wasp *Polistes fuscatus*. Proc R Soc London B 269(1499):1423–1428

Tibbetts EA (2006a) Badges of status in workers and gyne *Polistes dominulus* wasps. Ann Zool Fenn 43:575–582

Tibbetts EA (2006b) The condition-dependence and hereditability of signaling and non-signalling color traits in the paper wasps. Am Nat 175:495–503

Tibbetts EA (2008) Resource value and the context dependence of receiver behaviour. Proc R Soc London B 275:2201–2206

Tibbetts EA, Curtis TR (2007) Rearing conditions influence quality signals but not individual identity signals in *Polistes* wasps. Behav Ecol 18(3):602–607

Tibbetts EA, Dale J (2004) A socially enforced signal of quality in a paper wasp. Nature 432(7014):218–222

Tibbetts EA, Dale J (2007) Individual recognition: it is good to be different. Trends Ecol Evol 22(10):529–537

Tibbetts EA, Injaian A (2013) Preferential phenotypic association linked with cooperation in paper wasps. J Evol Biol 26:2350–2357

Tibbetts EA, Lindsay R (2008) Visual signals of status and rival assessment in *Polistes dominulus* paper wasps. Biol Lett 4(3):237–239

Tibbetts EA, Sheehan MJ (2011) Facial patterns are a conventional signal of agonistic ability in *Polistes exclamans* paper wasps. Ethology 117(12):1138–1146

Tibbetts EA, Shorter JR (2009) How do fighting ability and nest value influence usurpation contests in *Polistes* wasps? Behav Ecol Sociobiol 63:1377–1385

Tibbetts EA, Sheehan MJ, Dale J (2008) A testable definition of individual recognition. Trends Ecol Evol 23:356

Tibbetts EA, Mettler A, Levy S (2010) Mutual assessment via visual status signals in *Polistes dominulus* wasps. Biol Lett 6(1):10–13

Tibbetts EA, Izzo A, Huang ZY (2011a) Behavioral and physiological factors associated with juvenile hormone in *Polistes* wasp foundresses. Behav Ecol Sociobiol 65(5):1123–1131

Tibbetts EA, Skadina O, Zhao V, Thot AL, Skaldin M, Beani L, Dale J (2011b) Geographic variation in the status signals of *Polistes dominulus* paper wasps. PLoS One 6:e28173

Toth AL, Bilof KBJ, Henshaw MT, Hunt JH, Robinson GE (2009) Lipid stores, ovary development, and brain gene expression in *Polistes metricus* females. Insectes Soc 56:77–84

Turillazzi S (2012) The biology of hover wasps. Springer, Berlin

Turillazzi S, Cervo R (1982) Territorial behaviour in males of *Polistes nimpha* (Christ) (Hymenoptera, Vespidae). Zeitschrift für Tierpsychologie 58:174–180

Van Zweden JS, d'Ettorre P (2010) Nestmate recognition in social insects and the role of hydrocarbons. In: Blomquist GJ, Bagnères AG (eds) Insect hydrocarbons: biology, biochemistry and chemical ecology. Cambridge University Press, Cambridge, pp 222–243

Whiting MJ, Nagy KA, Bateman PW (2003) Evolution and maintenance of social status-signaling badges. Experimental manipulations in lizards. In: Fox SF, McCoy JK, Baird TA (eds) Lizard social behavior. JHU Press, Baltimore, pp 47–82

Wiley RH (2013) Specificity and multiplicity in the recognition of individuals: implication for the evolution os social behaviour. Biol Rev 88:179–195

Wilson EO (1971) The insect societies. Harvard University Press, Cambridge, p 548

Zanette L, Field J (2009) Cues, concessions, and inheritance: dominance hierarchies in the paper wasp *Polistes dominulus*. Behav Ecol 20(4):773–780

Chapter 9
Nestmate Recognition in Eusocial Insects: The Honeybee as a Model System

Michael D. Breed, Chelsea N. Cook, Helen F. McCreery and Michael Rodriguez

Abstract This review summarizes and evaluates the available information on honeybee nestmate recognition. Nestmate recognition is the ability of members of a colony to discriminate members of their own colony from others, particularly conspecifics, trying to enter the nest. Honeybee nestmate recognition is mediated by chemical cues that bees gain after emergence as adults. The comb wax in the nest is an important intermediary for transfer of cues among bees in the colony, resulting in a relatively uniform recognition profile which is carried by workers in the colony. Alkenes and free fatty acids are the primary chemical cues in the recognition profile. The ability of honeybees to discriminate nestmates from non-nestmates has raised the question of whether recognition mechanisms might exist to support nepotism within colonies. A variety of experimental approaches have failed to generate support for preferential behavior among highly related subgroups of bees in honeybee colonies. Other questions addressed in this review include queen recognition, response thresholds for expression of recognition, and sensory and information gathering aspects of the recognition system of honeybees. Nestmate recognition in honeybees is a valuable model system for the study of social recognition in animals.

Introduction

Social recognition is important in nest defense and territorial interactions, while also playing a role in decisions about within-colony aid giving, or nepotism. To engage in conflict among colonies, eusocial insect workers must discriminate between fellow colony members and workers from other colonies. For finer

M.D. Breed (✉) · C.N. Cook · H.F. McCreery · M. Rodriguez
Department of Ecology and Evolutionary Biology, The University of Colorado,
Boulder, CO 80309, USA
e-mail: michael.breed@colorado.edu

L. Aquiloni and E. Tricarico (eds.), *Social Recognition in Invertebrates*,
DOI 10.1007/978-3-319-17599-7_9

behavioral distinctions within colonies, social recognition cues must carry information about genetic relatedness. This chapter focuses on social recognition in the western honeybee, *A. mellifera*. We review how these abilities to discriminate are the basis for important types of social recognition in honeybees. While our review is limited to honeybees, many of the principles established in these studies have broad applicability to eusocial insects.

Honeybees are an example of eusocial insects, which also include ants, termites, some bees, some wasps and facultatively some thrips and aphids. The key element of eusociality is reproductive division of labor, in which one or a few reproductive individuals (in the case of honeybees, the queen) are responsible for most or all of the reproduction and a portion of the queen's offspring are sterile workers whose function is to enhance the reproduction of the queen. Eusocial species typically live in social groups called colonies and occupy physical structures termed nests. They may store food in their nests, yielding a resource that likely needs defense. The feeding home range around the nest may also be defended, extending the potential for aggression to territory boundaries.

The defense of food or home range requires that defenders can discriminate between their nestmates and potential marauders. Much of this review focuses on the ability of honeybees to discriminate nestmates from non-nestmates. Written accounts of conflict among eusocial insect colonies pre-date organized scientific approaches to behavior and ecology and wars among eusocial insect colonies form a strong part of the popular image of eusocial insect behavior. Social recognition is a key element of this type of intercolonial conflict.

Apiarists have long been keenly aware of aggressive encounters at honeybee nest entrances and the need for honeybee colonies to defend themselves against raids by other colonies. Early scientific interest in honeybee colony defense included Butler and Free's (1952) exploration of behavior at nest entrances and Kalmus and Ribbands' (1952) experiments on how floral odors might be used in social recognition by honeybee guards. The number of studies on these topics was modest until Hamilton's (1964) papers on kin selection stimulated further examinations of nestmate recognition in a variety of social insects (Greenberg 1979, see reviews by Breed and Bennett 1987 and in Vander Meer et al. 1998 and Starks 2004).

Key to social recognition in honeybees is exclusion of non-colony members from the nest. Certain bees, called guards, specialize in honeybee colony nest entrance defense. The guard bees often were not recorded in studies of honeybee division of labor that focused on marked age cohorts (Lindauer 1952). This was a reflection of the fact that a very small percentage of bees in a colony guard at any one time, so that if a few hundred bees are marked at emergence the chances that a bee within the sample would be observed guarding were small. Moore et al. (1987) used larger cohorts of marked bees to determine the age distribution of guards and the persistence of guards in this work. These observations of guard bees and their behavior led to an understanding of the important role of guards in excluding non-nestmates from their colony.

Honeybees do not express obvious nestmate recognition and territoriality at floral resources. This contrasts with some species of meliponine bee that defend floral resources as well as their nest (Breed et al. 2004a). This fact is important because it means that honeybee nests may be aggregated in areas with suitable nest sites (groves of hollow trees, caves, cliffs and rock overhangs) and forage on common resources. Aggregated nesting likely contributes to the tolerance of honeybees for being managed in apiaries ranging from a few to dozens of colonies. At times, honeybee colonies intensively rob other colonies, with weaker colonies losing resources to stronger colonies (Chapman et al. 2009). Many *Apis* species nest in aggregations. This proximity of nesting suggests some tolerance for nearby non-nestmate conspecifics, but which also suggests evolutionary motivations for being able to exclude non-nestmates from the nests, as proximity among nests likely increases the likelihood of theft of food resources.

Proximity of nests could also promote inquilinism. Inquilinism is a form of social parasitism in which an animal enters a colony and exploits the brood-rearing capabilities of the members of that colony, see Breed et al. (2012) for a discussion of the different types of social parasitism. A situation in which unaffiliated honeybee queens enter nests and take over reproduction would be a form of inquilinism. This type of inquilinism is known in yellowjackets, which are the wasp genus *Dolichovespula* (Carpenter and Perera 2006; Breed et al. 2012) and a variety of ants (Breed et al. 2012). Interestingly, inquilism by queens in honeybees has not been observed. The system of recognition of queens by honeybee workers, which is discussed as part of this review, may be responsible for the prevention of inquilism.

Combat among colonies and queen recognition are not the only context in which social recognition information can play a role for honeybees. Nepotism provides another potentially important platform for social insect workers to express social recognition. Hamilton's (1964a, b,) work stimulated investigators to explore the potential for social recognition to mediate nepotism within colonies (Boomsma and d'Ettorre 2013). There is enough genetic variance among workers within honeybee colonies due to multiple mating by queens to support a prediction that honeybee workers should sometimes favor larvae or adult workers to which they are more closely related than average within the colony (Hamilton 1964a, b). Specifically, workers are predicted under circumstances such as queen rearing to give preference to larvae with which they share a father; such preferences are considered to be nepotistic. The social recognition system required for this type of fine-tuned discrimination is dramatically different than a system that gives information about membership in the colony as a whole. Numerous studies, which are reviewed in a following section, have addressed the question of whether nepotism occurs in honeybee colonies.

In this chapter we refer to the western honeybee, *A. mellifera*, as "the honeybee". *A. mellifera* is the most cosmopolitan of the dozen or so members of the genus *Apis*, which has its center of diversity in Southeast Asia and Malaysia. Characters that unite the members of the genus include: having barbed dehiscent stings that remain in the victim after stinging, nests constructed of wax combs, storage of honey and pollen in those combs, and the use of dances to communicate the locations of food sources. *A. mellifera* has two important derived nesting characteristics—preferring to construct its nests in cavities, such as hollow trees, and making nests with multiple combs—that are shared with a similar Asian species, *Apis cerana*. Studies of nestmate recognition in *A. cerana* and other *Apis* species suggest that nestmate recognition is not as strongly expressed in those species as in *A. mellifera* (Breed et al. 2007; Tan et al. 2010; Holmes et al. 2013).

Honeybees are an economically important organism and the consequent focus on this species as a study organism has meant that different laboratories have had the time, resources and motivation to replicate studies; this has been much more the case in honeybees than any other social insect species. Independently replicated results add to the certainty of conclusions and also allow us to understand nuances of behavior that might be missed by investigators in a single laboratory using only the techniques available to them. Many of the questions approached in this review have been studied in more than one laboratory. Generally speaking, the original results for each question have been confirmed, but there are some interesting differences in evidence or interpretation, as well.

Following a background section on nestmate recognition in eusocial insects, we discuss each of the major themes—cue use in colony defense, queen recognition, and nepotism—mentioned above. Two more integrative topics, information processing and cue thresholds, are the subjects of the next two sections. In our discussion and conclusions we emphasize the need for a better understanding of how recognition information is neurologically processed. We also discuss the relevance of our knowledge of honeybee nestmate recognition to nestmate recognition systems in other eusocial insects.

Nestmate Recognition: Principles and Theory

Nestmate recognition is often characterized as a kind of kin recognition. Sometimes this characterization is correct and sometimes it is a mistake to think of nestmate and kin recognition as being synonymous. Strictly speaking, kin recognition is the ability to make discriminations among other animals based on identity by descent (Hamilton 1983) while nestmate recognition may use other mechanisms, such as non-genetic nest-specific odors. Hamilton (1983) emphasizes the evolutionary importance of being able to make fine distinctions based on relatedness. Within a eusocial insect colony, for example, a worker might use kin recognition information to choose which larvae to rear into queens (mentioned in Introduction). This distinction could be, for example, between supersisters (same mother and father as the worker, related on average by 0.75 in Hymenoptera) and half sisters (same mother but different father, related on average by 0.25 in Hymenoptera). Making fine distinctions requires that individuals present hypervariable recognition cue phenotypes that correlate with genetic background. Also required is the ability of members of the social group to perceive and process this detailed phenotypic information.

Some contexts that favor the evolution of individual-distinctive odors concern the queen, rather than the workers. One such circumstance, which is discussed below is the possibility that queen-specific cues might allow workers to sort according to their relatedness with queens during swarming. Another possibility, also discussed below, is that queen-specific odors might help workers to prevent parasitization by queens from other colonies or other species. Wenseleers et al. (2010) give an example of this type of social parasitization in a stingless bee. Genetically correlated cues that identify queens could then also be used by workers in discriminations among workers, even though this may not be the primary selective force that maintains the cues over generations.

Defense at a nest entrance is a different matter, because the choice is between whether an individual belongs in the nest or not. A simple yes–no categorization of membership can rely on far less phenotypic variation, and the phenotype does not need to be correlated with genotype to convey the information needed in order to make the discrimination. Non-belongers can include conspecific workers that have made an orientation mistake, conspecific workers that have arrived to rob resources, conspecific social parasites, heterospecific social parasites, and heterospecific predators or robbers. Answering the question of whether an arriving animal belongs in the colony or not only requires a simple cue or signal, uniform among colony members, that is unique to that colony with respect to other colonies in the same area (Fig. 9.1).

In most eusocial insects odor cues have primary importance in making social discriminations. Cuticular hydrocarbons have particular significance for social recognition as the cuticular hydrocarbon profile of any individual in a social

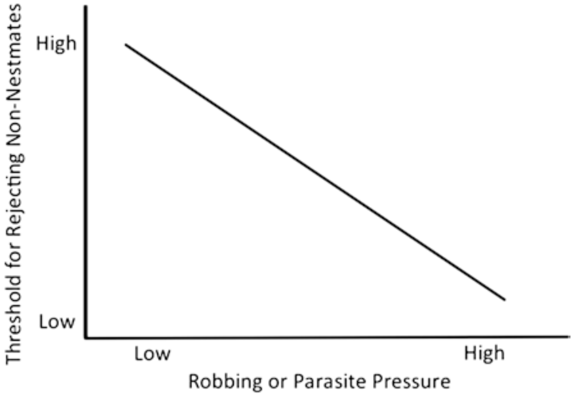


Fig. 9.1 The likelihood a guard will reject (attack) a bee arriving at a colony depends on the degree of match in chemical cues between the guard and the arriving bee. In this simple representation there is a linear relationship between match and rejection as observed by Greenberg (1979) in a halictid bee, *Lasioglossum zephyrum*. Depending on ecological circumstances and evolutionary history the guard response may vary to minimize the cost of errors (Reeve 1989). See below and work by Couvillon et al. (2009, 2012, 2013a, b) for more discussion of the implications of recognition errors

group contains many compounds, thus setting the stage for meeting the criterion of hypervariability necessary for making fine distinctions among kin. Cuticular hydrocarbon mixes typically include alkanes, methyl-branched alkanes, and alkenes. The first evolutionary role for cuticular hydrocarbons was to prevent desiccation of surface waxes, which prevent water loss. Hydrocarbons are almost universally found on terrestrial organisms (Drifjhout et al. 2010). A blend of surface hydrocarbon compounds helps to prevent water loss over a range of temperature conditions, working more effectively than if the wax layer were composed of a single compound. The complexity of the cuticular blend lends itself to co-option of these compounds for signal functions, such as sex pheromones (Drifjhout et al. 2010; van Zweden et al. 2010), queen-produced reproductive signals (Van Oystaeyen et al. 2014), and social recognition cues. In addition to prevention of water loss and signal functions, surface compounds may have antibiotic effects, and the possibility that any one compound in the cuticular mix may have multiple functions should not be ignored.

Investigations of surface waxes reveal that most insects present a mix of alkanes (van Zweden and d'Ettorre 2010). Lower molecular weight alkanes have the advantages of easily spreading on the insect surface but are subject to loss through to volatilization. Higher molecular weight alkanes are less likely to volatilize but may crystallize, particularly at lower ambient temperatures. A mixture of alkanes including lower molecular weight (C-16 or even smaller) and high molecular weight (up to C-40) compounds results in a surface coating that is malleable, flows enough to evenly cover the surface, but which resists volatilization. In some insects methyl-branched alkanes and alkenes are also present; these functional groups affect volatility and other physical characteristics of the hydrocarbon mix, but it is not clear if side chains or unsaturated bonds evolved in response to selective pressures for properties like dessication prevention or antibiotic effects. Among surface waxes, methyl-branched alkanes and alkenes are more often functional as social recognition cues than alkanes (Breed and Buchwald 2008). In bees, fatty acids, fatty acid esters, and macrocyclic lactones are also important cue compounds (Breed and Buchwald 2008). These and other cuticular hydrocarbons can provide information needed to make individual distinctions as well as kin discrimination.

Given the close proximity of individuals within the nest, surface chemicals may be easily transferred among animals. As a result, individual distinctions can become quite blurred. This is a positive outcome if the cue function of the surface chemicals is to convey colony membership, as the blending of cues among workers can result in a single, colony-level, recognition signal (Breed and Buchwald 2008). This is facilitated in ants by mixing of hydrocarbons in the postpharyngeal gland that facilitates the loss of individuality (Soroker and Hefetz 2000).

As pointed out above, a single colony-level phenotype is a more parsimonious solution for nestmate recognition, even though such a system may not contain information about kinship. This is essentially a bi-layer system of making distinctions: one for "I'll let you in" and one for "I'll promote your genes." Although they both fall under the general category of recognition, they represent distinct mechanisms. Cuticular hydrocarbons can provide more than adequate information for nestmate discrimination but may function better in this context if the cues are blended among animals in a nest so that a singular colony-unique identity emerges. In paper wasps blending of CHC among individuals occurs with the paper nest serving an intermediary (Gamboa et al. 1996). In stingless bees the nest similarly serves as an intermediary for recognition cues (Jones et al. 2012). This is true as well in the honeybee, which is discussed in detail below. The picture is more variable in ants, with nest materials being implicated in some ants as the source of recognition cues (Carlin and Holldobler 1986; Crosland 1989), other studies suggesting diet is important (Buczkowski and Silverman 2006), while in other ants the postpharyngeal gland serves as an intermediary for mixing of cues among individuals (Soroker and Hefetz 2000). For more on ant nestmate recognition, see the recent review by Sturgis and Gordon (2012).

One interesting possibility, raised by Breed and Buchwald (2008) is that a cuticular hydrocarbon cue profile that is informative about identity by descent may co-exist with a colony-level cue profile that results from blending cues or acquiring cues from the environment for nest-specific odors. Boulay et al. (2000) point out that worker individuality in hydrocarbon signature drives the need for frequent worker contact to establish a cohesive profile in *Camponotus fellah*, a species in which a colony-level blend of hydrocarbons serves for nestmate recognition. In honeybees differences in cuticular hydrocarbons among workers based on task in the colony are know (Kather et al. 2011) but it is unclear how these differences play into nestmate recognition.

A notable exception to the use of odor cues by eusocial insects for nestmate recognition is a species of paper wasp, *Polistes fuscatus*, which uses visual phenotypes for individual recognition in discriminating individuals based upon facial markings (Sheehan and Tibbetts 2011). These visual phenotypes have the characteristics of hypervariability necessary for individual recognition. This use of visual phenotype is, as far as is known, unique to this wasp among eusocial insects.

Cues in Honeybee Nestmate Recognition

Kalmus and Ribbands (1952) raised the question of whether guards at honeybee colony entrances employ recognition cues that come from within the colony to discriminate nestmates from non-nestmates, or if they use environmentally derived odors to make the discrimination (Fig. 9.2). Their hypothesis was that if each colony forages on a unique mix of flowers, a colony odor results that gives the guards the information needed to detect colony membership. A potential flaw in this reasoning is that a forager returning from a new food source could be targeted for rejection by the guards. However, foragers returning with nectar that are harassed by guards often offer nectar to the guards, a behavior which short-circuits the potential for rejection. Kalmus and Ribbands (1952) and Ribbands (1953) reported that when colonies were paired and one was treated with a strong

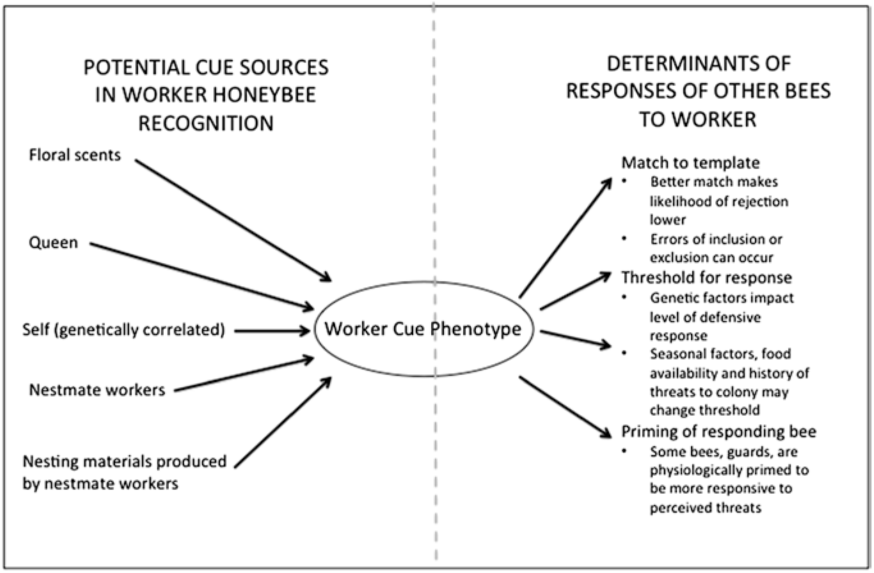


Fig. 9.2 The possible sources of chemical cues on the surface of a honeybee worker (*left side* of figure) and how other bees, particularly guards, might use that information (*right side* of figure)

food odor that guard discrimination between members of the two colonies was enhanced. Bowden et al. (1998) and Downs et al. (2000, 2001) revisited the question of whether floral oils affect nestmate discrimination by honeybee guards. Both of these studies reported negative results, suggesting that other cue sources are more important in honeybee nestmate recognition.

Following publication of the Kalmus and Ribbands (1952) study little attention was paid to nestmate recognition and guard behavior in honeybees until Breed (1983 and later publications) took up this topic in response to a reawakening of interest in the study of social recognition and kin discrimination that was sparked by Hamilton's (1964a, b) papers on kin selection. Greenberg's (1979) work on a halictid bee, *Lasioglossum zephyrum*, suggested that testing hypotheses about genetic correlations with recognition cues could be fruitful, and gas chromatographic analyses of the surface chemistry of a variety of insects had demonstrated considerable cuticular compound diversity within insect species, suggesting that the basis for recognition cues might be present in cuticular hydrocarbons (Smith 1983; Smith and Breed 1995; Drijfhout et al. 2010; van Zweden and d'Etorre 2010).

Breed's (1983) study suggested a genetic basis for colony odors in honeybees. Subsequent experiments showed that: (1) Recognition cues can be transferred among bees via wax (Breed et al. 1998, 1988a), (2) Workers acquire recognition cues within the first few days after adult emergence (Breed et al. 1988b, 2004b),

(3) Workers can discriminate, by odor, among wax combs from different colonies and exhibit an orientation preference for comb that they have lived on for at least a few days (Breed et al. 1995c; Breed 1998a, b), (4) Variation of cuticular hydrocarbons among colonies and among wax combs is correlated with genetic differences among colonies (Breed et al. 1995a; Breed 1998a, b), (5) Unsaturated fatty acids which are incorporated into beeswax as the comb is constructed are critical recognition cues for worker honeybees (Breed et al. 1995a, b; Breed 1998a, b; Lyon et al. 2012), (6) Alkenes from the cuticular hydrocarbon mix also function as recognition cues (Breed and Julian 1992), (7) Tests of the role of alkanes as recognition cues have yielded some negative results (Breed and Stiller 1992) and some positive results (Dani et al. 2005; Chaline et al. 2005). Ratnieks et al. (2011) argued that contact among honeybees does not affect acceptance of non-nestmates by guards, and this result may be consistent with the importance of wax comb, rather than workers "rubbing shoulders" in transferring nestmate recognition cues.

Adequate cues for assessing the presence of non-nestmates exist in the air around bees (Mann and Breed 1997 and references therein), a point that should be given more careful consideration in future studies of honeybee nestmate recognition. An important but overlooked study by Stabentheiner et al. (2002) clearly shows that the thermal profile of incoming honeybees at colony entrances can affect their presentation of nestmate recognition cues, as the temperature of these bees is adequate to volatilize compounds that might not be considered volatile enough to serve as cues at ambient temperatures.

Guard response thresholds to intruding workers, which we discuss later, vary seasonally and guards are more responsive during times when robbing among colonies is higher (Couvillon and Ratnieks 2008; Downs and Ratnieks 2000). Perhaps most notable in the long sequence of publications on nestmate recognition in honeybees is that researchers have independently verified most of the key findings, such as the role of comb wax in honeybee nestmate recognition (Breed et al. 1995c; Breed 1998a, b) re-tested first by Tyus (1998), then by D'Etorre et al. (2006), and finally by Couvillon et al. (2007). The wax odor is a result of glandular products of the bees incorporated into the comb during its construction (Buchwald et al. 2009).

Couvillon et al. (2009, 2012, 2013a, b) have focused on recognition errors made by guard bees (Fig. 9.3). Among their interesting findings are that testing context affects error rates (Couvillon et al. 2013a, b) and that error rates may suggest how to interpret models of information use in nestmate recognition (Couvillon et al. 2009, 2012).

In sum, honeybee nestmate recognition fits into a pattern of homogenization of nestmate recognition cues through an intermediate structure, in this case the wax combs. The multiple independent replications of this finding (Breed et al. 1995a, b, 1998; Tyus 1998, D'Etorre et al. 2006, Couvillon et al. 2007) give a great deal of certainty to this conclusion.

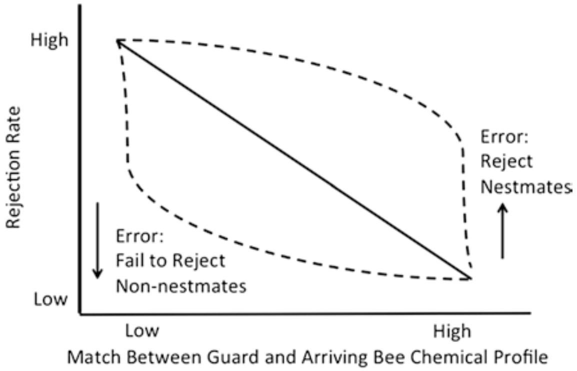


Fig. 9.3 Errors in recognition are potentially caused by variation in recognition cues, so that colony mates may be more dissimilar than random selected pairs of bees from the colony or non-nestmates may be more similar to a guard than the mean difference in recognition cue profiles between the colony and other colonies in the population. The linear response model (*solid line*) implies a graded response depending on degree of match between the guard and the arriving bee. In fact, guard responses are usually interpreted as bimodal: either attack or accept. This bimodality suggests inflected curves for the relationship between rejection probability and the guard/arriver match (*dashed lines*). The *upper dashed line* illustrates low tolerance for variance from the colony's cues, resulting in errors involving rejection of nestmates. The *lower dashed line* represents high tolerance for mismatches, resulting in errors involving acceptance of non-nestmates

Queen Recognition

Queen recognition is fundamentally different than discrimination of workers, as honeybee colonies typically contain only one queen; it is feasible and likely desirable from an evolutionary point of view for workers bees in a colony to be able to recognize their queen as an individual (Breed 1981; Fan et al. 2010). In *A. cerana* potential inquilines exist but guards cannot discriminate between robbers and inquilines (Holmes et al. 2013).

A primary selective advantage of workers being able to recognize the queen of their colony as an individual is that this might facilitate identification and elimination of potential social parasites. An interesting feature of honeybee biology is that social parasitism in the form of inquilinism is very infrequently observed. Two forms of inquilinism might be imagined in honeybees: (1) Unaffiliated queens entering and usurping a colony or (2) Another species of bee that specializes in parasitizing honeybee colonies might come in and exploit the labor and food available in a honeybee colony. Organisms other than honeybees, for example wax moths, *Galleria mellonella* and *Achroia grisella*, may also enter the colony and exploit resources. Both of these types of inquilinism exist in other bee species and in many ant species. Unaffiliated conspecific usurpers are known in *Dolichovespula* wasps, and the second type of inquilinism is illustrated by *Psithyrus* female workers in *Bombus* colonies and *Paralictus* female workers in *Lasioglossum* colonies.

Boch and Morse (1979) first explored the question of individual recognition of queens by workers in honeybees. Their results clearly support the ability of swarms to identify their own queen and to aggregate around her. Breed (1981) elaborated on this discovery by finding that honeybee workers use genetically correlated chemical cues to make discriminations among queens, a finding that was independently replicated by Boch and Morse (1982). All of these studies support the hypothesis that chemical cues, specifically odors, are responsible for the ability of workers to make these discriminations (Boch and Morse 1981). Breed et al. (1992) tested the effects of fatty acid esters found in queen feces on the ability of workers to discriminate among workers. The positive findings from this study of fatty acid esters suggest that perhaps they play a role in queen recognition, although this is a result that strongly suggests follow-up studies, rather than a conclusive demonstration that these esters play this role.

In cape honeybees, *Apis mellifera capensis*, workers can assume a queen-like role within a colony, laying eggs that will develop into females via a unique (within the genus *Apis*) mechanism of thelytokous parthenogenesis. Competition among laying workers (Beekman and Oldroyd 2008) and policing of laying activities by non-laying workers (Pirk et al. 2003) has some similarity to behavioral patterns associated with inquilinism. In particular, the tendency of workers to eliminate other laying workers is a behavior that would be equally effective in regulating the entry of queens from other colonies into a nest. The cape bee, however, does not represent an example of social parasitism in *Apis,* but simply illustrates the presence of mechanisms that could be effective in preventing inquilinism in one subspecies within the genus.

The virtual absence of social parasitism in *A. mellifera* seems unusual among the eusocial insects, in which examples of conspecific and interspecific social parasitism are common. The nest structures and social behavior of members of this genus suggest only one specific barrier to social parasitism, worker policing of eggs laid by other workers (Ratnieks and Visscher 1989). One line of reasoning, although purely speculative, for why inquilinism is perhaps rarer in *Apis* than in other eusocial insects is that the mechanism of queen recognition in *Apis* is effective enough to serve as a strong selective force against the evolution of this type of social parasite. Or, perhaps, many inquilines exist in *Apis* and simply remain undiscovered.

Nepotism

Two primary hypotheses for nepotism have been explored in honeybees. Both stem from the fact that honeybee queens mate ten to fifteen times early in their adult lives and use stored sperm from these matings in egg fertilization through their life. Thus, all the workers in a honeybee colony are daughters of a single queen, but the worker population is divided into subgroups, patrilines, each representing drones that mated with the queen. Following kin selection theory, workers should favor their own patriline over other patrilines if reproduction would be affected by this nepotism (Boomsma and d'Ettorre 2013). In order to express such favoritism social recognition must come into play for the workers; they would need to be able to discriminate eggs and larvae, adult workers, or queens by patriline membership.

The first hypothesis tested concerning nepotism in honeybees was that workers would sort by subfamily group during swarming. The principle underlying this hypothesis is that since the new queen reared by a colony will represent only one of the several possible fathers in the colony, selection should favor workers that can choose to work for the new queen, if she is from their patriline. The remaining workers are equally related to the old queen, their mother, and the new queen, their half-sister, and they should assort randomly between the two queens at swarming time. Getz et al. (1982) found evidence for this assortment, but subsequent studies did not replicate this result (Kryger and Moritz 1997; Rangel et al. 2009).

A second set of hypotheses about nepotism in honeybees center on selection of eggs or young larvae for queen rearing. Of the hundreds or thousands of female eggs or larvae in a honeybee colony at any given point in time during the spring and summer, only a few are selected for rearing into queens. Studies on this type of nepotism in honeybees conducted between 1970 and 1990 showed that workers did not preferentially direct their behavior to their most highly related eggs and larvae and found no support for the hypothesis that workers rear queens that are more closely related to them as a result of selecting genetically matching larvae for queen rearing (Breed et al. 1984; Visscher 1986, see also review by Breed et al. 1994). Rangel et al. (2009) used more contemporary genetic techniques to test the hypothesis of within colony nepotism and obtained negative results, as did Koyama et al. (2009). On the other hand, worker policing has the potential for removing evidence for kin-biased behavior through the destruction of eggs that represent the workers', rather than the queen's, genetic interests (Visscher and Ratnieks 1989).

Breed et al. (1995c) looked at this same type of question of within colony nepotism in interactions among adult workers using color phenotypes as a proxy for genetic identification of subfamilies. Breed et al. (1994) also demonstrated that, in the absence of comb wax cues workers could express an ability to preferentially associate with more related workers. However, these findings did not establish a direct link to the behavior of bees in more naturally constructed colonies, and it was not clear from these results whether this type of social recognition persists in the presence of comb wax.

The question of nepotism in eusocial insect colonies has been addressed in other species, as well. Several studies of ants have noted an absence of nepotistic behavior within colonies (Zinck et al. 2009; Kellner and Heinze 2011; Friend and Bourke 2012). In eusocial wasps the chemical information necessary for discrimations that would support nepotism is available, at least in some species (Dani et al. 2004) and data suggests that this information can be used in *Polistes dominulus* (Leadbeater et al. 2014). The negative results in honeybees and ants in the search for evidence of nepotism do not preclude the possibility that further studies using different methods might reveal nepotism in these species. However, the fact that the negative result has been repeatedly obtained by different investigators using a variety of methods suggest that the likelihood of this is small.

Information Processing and Discriminations

Surprisingly few studies address how recognition information is perceived and processed in honeybees, or for that matter, in social insects in general. Crozier and Dix (1979) and Getz (1982) explored models for how recognition information might be processed by guards at nest entrances of eusocial insects. A key element of their models was consideration of what rules social insects might use in making nestmate-non-nestmate discriminations. The models also considered how alleles might match with odor cues, so that population genetic models could be applied to analyses of cue evolution. Breed and Buchwald (2008) summarized these earlier modeling efforts and discuss their implications in light of improved knowledge about the chemical cues involved in nestmate recognition.

Few papers have explored the details of how potential information in surface compounds on insects might translate into actual usage by workers to make discriminations. Breed et al. (2004c) presented bees with differing ratios of free fatty acids in a nestmate recognition bioassay and found that bees could possibly make use of information concerning compound ratios, but the data suggested that the information is processed in the context of the presence of other cues. Costanzi et al. (2013) explore how changes in cuticular hydrocarbon proportions affect nestmate recognition in a social wasp.

Another theoretical issue is whether the information present is adequate to make the hypothesized discriminations. For example, an investigator might hypothesize abilities of worker bees to discriminate subfamily membership, age, and current task of other bees, but is the variation in surface chemistry among bees organized in ways that allow all of these discriminations? This is not known in honeybees, but in the sweat bee *Lasioglossum malachurum* Soro et al. (2011) found a weak correlation between cuticular chemistry and the genetic distance among bees. This variation is not adequate to support within colony discriminations based on relatedness (Soro et al. 2011). Breed and Buchwald (2008) modeled how olfactory and neural abilities predict the number of compounds available for discrimination; they found that if an animal can make moderately fine distinctions among compound concentrations, rather than just assess the presence or absence of a compound, then eight to ten cue compounds in a cue profile should be adequate for discriminations among colonies. This matches well with the number of relatively abundant alkenes and free fatty acids on the surface of honeybees. There are also quite a few alkanes on bees, but the use of these in discrimination is less likely (Breed and Stiller 1992), but see Chaline et al. (2005) for a conflicting point of view.

Response Thresholds

One of the major conflicts in our understanding of honeybee nest defense is between our knowledge of the ability of honeybees to discriminate nestmates from non-nestmates and the common observation that honeybee workers “drift” among colonies, resulting in much larger worker forces in downwind colonies in apiaries. In part the explanation for this seeming contradiction comes from understanding that the threshold for expression of defensive behavior by honeybees depends on season and food availability (Reeve 1989). The presence of drift was well known among beekeepers and early studies on nestmate recognition in honeybees may have overly discounted the potential importance of drift as a symptom of laxity or flexibility in the social recognition system of honeybees. Given the number of species of *Apis* that nest in aggregations, the tolerance of drift in *A. mellifera* is a bit surprising, as drifting workers could represent potential robbers or inquilines (Chapman et al. 2010). Speculatively, the tolerance of drift in *A. mellifera* could either represent the result of selection balancing the costs and benefits of excluding non-nestmates.

Discussion and Conclusions

Social recognition in *A. mellifera* operates on several levels. The best studied contexts are recognition of queens and discrimination of nestmates from non-nestmates. Queens are recognized individually and fatty acid esters have been implicated, but not conclusively tested, as queen recognition cues. Nestmate workers are discriminated from non-nestmates using cues transmitted via the comb wax. Candidate cue compounds include fatty acids, which are strongly supported by data, alkenes, which also have strong support, and alkanes, which are less well supported as cue compounds. Variation in compound concentrations for all three of these classes is significant among combs from different colonies, suggesting that nestmate recognition includes some genetic information. More detailed information about individual bees may be held in chemical signatures that underlay the colony-level signature. This could include information about age, task performance, and potential reproductive status, but this form of social recognition is less well investigated in honeybees. The use of nesting materials as an intermediary in nestmate recognition has analogies with other social insects, including paper wasps and some species of ants. This commonality suggests an evolutionary thread that favors group over individual recognition under at least some circumstances.

However, there are underlying differences in surface chemistry among honeybees, even among nestmates, that in theory could support kin recognition and nepotism. The numerous papers published on nepotism in honeybees report studies that on the whole do not support hypotheses of preferential allocation of resources within honeybee colonies through identity by descent. It appears that fine discrimination information is not perceived by honeybees, is perceived but not used, or is perceived and used in as yet unmeasured ways.

One aspect of the commentary that developed about nestmate recognition as a form of social recognition was that many investigators made an argument that nestmate recognition must be a form of kin recognition. This line of reasoning noted that nestmates are usually genetic relatives. However, the ability to discriminate a nestmate from a non-nestmate does not necessarily equip a social insect worker to make finer distinctions based on identity by descent, which is a reasonable requisite for kin recognition. Nepotism within colonies should, based on kin selection theory, be based on such fine discriminations and requires a recognition system in which the recognition phenotype is correlated with genetic identity. As our picture of honeybee nestmate recognition developed over the last 30 years it has become apparent that selection has favored uniformity of nestmate recognition cues among nestmate honeybees, rather than the phenotypic diversity required to make within colony distinctions.

Perhaps the most interesting aspect of this field of research is that researchers have been interested and motivated enough to re-test each other's hypotheses and to deeply explore the interaction between experimental design and result. Few areas in animal behavior and behavioral ecology have been so rich with efforts to determine the repeatability of experimental results. Most interpretations have withstood time and re-testing, but there is still much work to be done in understanding how guards as well as policing workers process and use information, as well as the exact cues they use in making discriminations.

References

Beekman M, Oldroyd BP (2008) When workers disunite: intraspecific parasitism by eusocial bees. Ann Rev Entomol 53:19–37

Boch R, Morse RA (1979) Individual recognition of queens by honey bee swarms. Ann Entomol Soc Am 72:51–53

Boch R, Morse RA (1981) Effects of artificial odors and pheromones on queen discrimination by honey bees (*Apis mellifera* L) (Hymenoptera, Apidae). Ann Entomol Soc Am 74:66–67

Boch R, Morse RA (1982) Genetic factor in queen recognition odors of honey bees. Ann Entomol Soc Am 75:654–656

Boomsma JJ, d'Ettorre P (2013) Nice to kin and nasty to non-kin: revisiting Hamilton's early insights on eusociality. Biol Lett 9:20130444

Boulay R, Hefetz A, Soroker V et al (2000) *Camponotus fellah* colony integration: worker individuality necessitates frequent hydrocarbon exchanges. Anim Behav 59:1127–1133

Bowden RM, Williamson S, Breed MD (1998) Floral oils: their effect on nestmate recognition in the honey bee, *Apis mellifera*. Insectes Soc 45:209–214

Breed MD (1981) Individual recognition and learning of queen odors by worker honeybees (*Apis mellifera*). Proc Nat Acad Sci USA 78:2635–2637

Breed MD (1983) Nestmate recognition in honeybees. Anim Behav 31:86–91

Breed MD (1987) Kin recognition in highly eusocial insects. In: Fletcher DJC, Michener CD (eds) Kin recognition in animals, Wiley, New York, pp 243–285

Breed MD (1998a) Chemical cues in kin recognition: Criteria for identification, experimental approaches, and the honey bee as an example In Chemical communication in social insects, R K Vander Meer, M L Winston, K E Espelie and M D Breed, eds Westview Press: Boulder, pp 57–78

Breed MD (1998b) Recognition pheromones on the honey bee. Bioscience 48:463–470

Breed MD, Bennett B (1987) Kin recognition in highly eusocial insects. In: Fletcher DJC, Michener CD (eds) Kin recognition, Wiley, New York, pp 243–285

Breed MD, Buchwald R (2008) Cue diversity and social recognition. In: Gadau J, Fewell JH (eds) Organization of insect societies, Harvard University Press, Cambridge, pp 171–192

Breed MD, Julian G (1992) Honey bee nestmate recognition: simple rules do not apply. Nature 357:685–686

Breed MD, Stiller TM (1992) Honey bee *Apis mellifera*, nestmate discrimination: hydrocarbons effects and the evolutionary implications of comb choice. Anim Behav 43:875–883

Breed MD, Velthuis HHW, Robinson GE (1984) Do worker honey bees discriminate among larval genotypes? Ann Entomol Soc Am 77:737–739

Breed MD, Fewell JH, Williams KR (1988a) Wax mediates the acquisition of honey bee nestmate recognition cues. Proc Nat Acad Sci USA 85:8766–8769

Breed MD, Stiller TM, Blum MS, Page RE Jr (1992) Honey bee nestmate recognition: effects of queen fecal pheromones. J Chem Ecol 18:1633–1640

Breed MD, Welch CK, Cruz R (1994) Kin discrimination within honey bee colonies: An analysis of the evidence. Behav Processes 33:25–40

Breed MD, Garry MF, Pearce AN, Bjostad L, Hibbard B, Page RE (1995b) The role of wax comb in honey bee nestmate recognition: genetic effects on comb discrimination, acquisition of comb cues by bees, and passage of cues among individuals. Anim Behav 50:489–496

Breed MD, Page RE Jr, Bjostad L, Hibbard B (1995c) Genetic components of variation in comb wax hydrocarbons produced by honey bees. J Chem Ecol 21:1329–1338

Breed MD, Leger EA, Pearce AN, Wang YJ (1998) Comb wax effects on the ontogeny of honey bee nestmate recognition. Anim Behav 55:13–20

Breed MD, Guzmán-Novoa E, Hunt GJ (2004a) Defensive behavior of honey bees: organization, genetics, and comparisons with other bees. Ann Rev Entomol 49:271–298

Breed MD, Perry S, Bjostad LB (2004b) Testing the blank slate hypothesis: why honey bee colonies accept young bees. Insectes Soc 51:12–16

Breed MD, Diaz PH, Lucero KD (2004c) Behavioural tests of models for information processing in nestmate recognition by honey bees, *Apis mellifera*. Anim Behav 68:921–928

Breed MD, Deng X-B, Buchwald R (2007) Comparative nestmate recognition in Asian honey bees, Apis florea, *Apis andreniformis*, *Apis dorsata*, and *Apis cerana*. Apidologie 38:411–418

Breed MD, Cook C, Krasnec MO (2012) Cleptobiosis in social insects Psyche, Article ID 484765, p 7

Buchwald R, Breed MD, Bjostad L, Hibbard BE, Greenberg AR (2009) The role of fatty acids in the mechanical properties of beeswax. Apidologie 40:585–594

Buczkowski G, Silverman J (2006) Geographical variation in Argentine ant aggression behaviour mediated by environmentally derived nestmate recognition cues. Anim Behav 71:327–335

Butler CG, Free JB (1952) The behaviour of worker honeybees at the hive entrance. Behaviour 4:262–292

Carlin NF, Holldobler B (1986) The kin recognition system of carpenter ants (*Camponotus spp*) 1. Hierarchical cues in small colonies. Behav Ecol Sociobiol 19:123–134

Carpenter JM, Perera EP (2006) Phylogenetic relationships among yellowjackets and the evolution of social parasitism (Hymenoptera : Vespidae, Vespinae). Am Mus Novitates 3507:1–19

Chaline N, Sandoz JC, Martin SJ, Ratnieks FLW, Jones GR (2005) Learning and discrimination of individual cuticular hydrocarbons by honeybees (*Apis mellifera*). Chem Senses 30:327–335

Chapman NC, Makinson J, Beekman M et al (2009) Honeybee, *Apis mellifera*, guards use adaptive acceptance thresholds to limit worker reproductive parasitism. Anim Behav 78:1205–1211

Chapman NC, Beekman M, Oldroyd BP (2010) Worker reproductive parasitism and drift in the western honeybee *Apis mellifera*. Behav Ecol Sociobiol 64:419–427

Costanzi E, Bagneres A-G, Lorenzi MC (2013) Changes in the hydrocarbon proportions of colony odor and their consequences on nestmate recognition in social wasps. PLOS One 8:e65107

Couvillon MJ, Ratnieks FLW (2008) Odour transfer in stingless bee marmelada (*Frieseomelitta varia*) demonstrates that entrance guards use an "undesirable-absent" recognition system. Behav Ecol Sociobiol 62:1099–1105

Couvillon MJ, Caple JP, Endsor SL et al (2007) Nestmate recognition template of guard honeybees (*Apis mellifera*) is modified by wax comb transfer. Biol Lett 3:228–230

Couvillon MJ, Roy GGF, Ratnieks FLW (2009) Recognition errors by honey bee (*Apis mellifera*) guards demonstrate overlapping cues in conspecific recognition. J Apic Res 48:225–232

Couvillon MJ, van Zweden JS, Ratnieks FLW (2012) Model of collective decision-making in nestmate recognition fails to account for individual discriminator responses and non-independent discriminator errors. Behav Ecol Sociobiol 66:339–341

Couvillon MJ, Segers FH, Cooper-Bowman R, Truslove G, Nascimento DL, Nascimento FS, Ratnieks FL (2013a) Context affects nestmate recognition errors in honey bees and stingless bees. J Exp Biol 216:3055–3061

Couvillon MJ, Segers Francisca HID, Cooper-Bowman R et al (2013b) Context affects nestmate recognition errors in honey bees and stingless bees. J Exp Biol 216:3055–3061

Crosland MJW (1989) Kin recognition in the ant *Rhytidoponera confusa* 2. Gestalt odor Anim Behav 37:920–926

Crozier RH, Dix MW (1979) Analysis of two genetic models for the innate components of colony odor in social Hymenoptera. Behav Ecol Sociobiol 4:217–224

Dani FR, Foster KR, Zacchi F, Seppa P, Massolo A, Carelli A, Arevalo E, Queller DC, Strassmann JE, Turillazzi S (2004) Can cuticular lipids provide sufficient information for within-colony nepotism in wasps? Proc Roy Soc B Biol Sci 271:745–753

Dani FR, Jones GR, Corsi S et al (2005) Nestmate recognition cues in the honey bee: differential importance of cuticular alkanes and alkenes. Chem Senses 30:477–489

D'Ettorre P, Wenseleers T, Dawson J et al (2006) Wax combs mediate nestmate recognition by guard honeybees. Anim Behav 71:773–779

Downs SG, Ratnieks FLW (2000) Adaptive shifts in honey bee (*Apis mellifera* L) guarding behavior support predictions of the acceptance threshold model. Behav Ecol 11:326–333

Downs SG, Ratnieks FLW, Jefferies SL et al (2000) The role of floral oils in the nestmate recognition system of honey bees (*Apis mellifera* L). Apidologie 31:357–365

Downs SG, Ratnieks FLW, Badcock NS et al (2001) Honeybee guards do not use food-derived odors to recognize non-nestmates: a test of the odor convergence hypothesis. Behav Ecol 12:47–50

Drijfhout FP, Kather R, Martin SJ (2010) The role of cuticular hydrocarbons in insects. In: Zhang W, Liu H (eds) Behavioral and chemical ecology, pp 91–114

Fan YL, Richard FJ, Rouf N, Grozinger CM (2010) Effects of queen mandibular pheromone on nestmate recognition in worker honeybees, *Apis mellifera*. Anim Behav 79:649–656

Friend LA, Bourke AFG (2012) Absence of within-colony kin discrimination in a multiple-queen ant, *Leptothorax acervorum*. Ethology 118:1182–1190

Getz WM (1982) An analysis of learned kin recognition in Hymenoptera. J Theor Biol 99:585–597

Getz WM, Bruckner D, Parisian TR (1982) Kin structure and the swarming behavior of the honey bee *Apis mellifera*. Behav Ecol Sociobiol 10:265–270

Greenberg L (1979) Genetic component of bee odor in kin recognition. Science 206:1095–1097

Holmes MJ, Tan K, Wang Z, Oldroyd BP, Beekman M (2013) Honeybee (*Apis cerana*) guards do not discriminate between robbers and reproductive parasites. Insectes Soc 60:265–271

Jones SM, van Zweden JS, Grueter C et al (2012) The role of wax and resin in the nestmate recognition system of a stingless bee, *Tetragonisca angustula*. Behav Ecol Sociobiol 66:1–12

Kalmus H, Ribbands CR (1952) The origin of the odors by which honeybees distinguish their companions. Proc Roy Soc B 140:50–59

Kather R, Drijfhout Falko P, Martin SJ (2011) Task group differences in cuticular lipids in the honey bee *Apis mellifera*. J Chem Ecol 37:205–212

Kellner K, Heinze J (2011) Absence of nepotism in genetically heterogeneous colonies of a clonal ant. Ethology 117:556–564

Koyama S, Takagi T, Martin SJ, Yoshida T, Takahashi J (2009) Absence of reproductive conflict during queen rearing in *Apis cerana*. Insectes Soc 56:171–175

Kryger P, Moritz RFA (1997) Lack of kin recognition in swarming honeybees (*Apis mellifera*). Behav Ecol Sociobiol 40:271–276

Leadbeater E, Dapporto Turillazzi S, Field J (2014) Available kin recognition cues may explain why wasp behavior reflects relatedness to nestmates. Behav Ecol 25:344–351

Lindauer M (1952) Ein Beitrag zur Frage der Arbeitsteilung im Bienenstaat. Z Vergl Psychol 36:299–345

Lyon C, Buchwald R, Breed MD (2012) The use of flax oil to influence honeybee nestmate recognition. J Econ Entomol 105:1145–1148

Mann CA, Breed MD (1997) Olfaction in guard honey bee discrimination of non-nestmates. Ann Entomol Soc Am 90:844–847

Moore AM, Breed MD, Moor MJ (1987) The guard honey bee; ontogeny and behavioral variability of workers performing a specialized task. Anim Behav 35:1159–1167

Pirk CWW, Neumann P, Ratnieks FLW (2003) Cape honeybees, *Apis mellifera capensis*, police worker-laid eggs despite the absence of relatedness benefits. Behav Ecol 14:347–352

Rangel J, Mattila HR, Seeley TD (2009) No intracolonial nepotism during colony fissioning in honey bees. Proc Roy Society B 276:3895–3900

Ratnieks FLW, Visscher PK (1989) Worker policing in the honeybee. Nature 342:796–797

Ratnieks FLW, Kaercher MH, Firth Verity et al (2011) Acceptance by honey bee guards of non-nestmates is not increased by treatment with nestmate odours. Ethology 117:655–663

Reeve HK (1989) The evolution of conspecific acceptance thresholds. Am Nat 133:407–435

Sheehan MJ, Tibbetts EA (2011) Specialized face learning is associated with individual recognition in paper wasps. Science 334:1272–1275

Smith BH (1983) Recognition of female kin by male bees through olfactory signals. Proc Natl Acad Sci USA 80:4551–4553

Smith BH, Breed MD (1995) The chemical basis for nestmate recognition and mate discrimination in social insects. In: Carde RT, Bell WJ (eds) Chemical ecology of insects II. Chapman and Hall, New York, pp 287–317

Soroker V, Hefetz A (2000) Hydrocarbon site of synthesis and circulation in the desert ant *Cataglyphis niger*. J Insect Physiol 46:1097–1102

Stabentheiner A, Kovac H, Schmaranzer S (2002) Honeybee nestmate recognition: the thermal behaviour of guards and their examinees. J Exp Biol 205:2637–2642

Starks PT (2004) Recognition systems. Ann Zool Fenn 41(6):689–892

Starks PT, Fischer DJ, Watson RE et al (1998) Context-dependent nestmate-discrimination in the paper wasp, *Polistes dominulus*: a critical test of the optimal acceptance threshold model. Anim Behav 56:449–458

Sturgis SJ, Gordon DM (2012) Nestmate recognition in ants (Hymenoptera: Formicidae): a review. Myrmecol News 16:101–110

Tan K, Wang ZW, Yang MX, Hepburn R, Radloff S (2010) Nestmate recognition differences between honeybee colonies of *Apis cerana* and *Apis mellifera*. J Insect Behav 23:381–388

Tyus HM (1998) Comb exchange as an aid in uniting honey bee colonies. Am Bee J 138:669–671

Van Oystaeyen A, Oliveira RC, Holman L, van Zweden JS, Romero C, Oi CA, d'Ettorre P, Khalesi M, Billen J, Wäckers F, Millar JG, Wenseleers T (2014) Conserved class of queen pheromones stops social insect workers from reproducing. Science 343:287–290

van Zweden JS, d'Ettorre P (2010) Nestmate recognition in social insects and the role of hydrocarbons. In: Blomquist GJ, Bagneres AG (eds) insect hydrocarbons: Biology, Biochemistry, and Chemical Ecology, pp 222–243

Vander Meer RM, Breed MD, Winston ML, Espelie KE (eds) (1998) Pheromone communication in social insects. Westview Press, Boulder, p 368

Visscher PK (1986) Kinship discrimination in queen rearing by honey bees (*Apis mellifera*). Behav Ecol Sociobiol 18:453–460

Wenseleers T, Alves DA, Francoy TM, Billen J, Imperatriz-Fonseca VL (2010) Intraspecific queen parasitism in a highly eusocial bee. Biol Lett 2010:0819

Zinck L, Chaline N, Jaisson P (2009) Absence of nepotism in worker-queen care in polygynous colonies of the ant *Ectatomma tuberculatum*. J Ins Behav 22:196–204

Chapter 10
Ontogeny of Nestmate Recognition in Social Hymenoptera

Lisa Signorotti, Rita Cervo and Patrizia d'Ettorre

Abstract The ability to discriminate between friends and foes is a central feature of social life. In social insects, nestmate recognition is mediated by colony specific cuticular hydrocarbons (CHCs) (label) that are perceived by an individual and compared with its neural representation of the colony odour (template). Although numerous advances have been made in understanding the identity, origin and production of recognition cues in social hymenoptera, relatively little is known about the ontogeny of nestmate recognition, and the learning processes that might be involved. It appears that wasps and bees learn the recognition cues required for template formation from their nest/comb odour, while ants learn principally from their nestmates. In general, the referent template is learned during the early stages of adult life, although pre-imaginal learning might play a role. The CHC blend can change over time; cue-exchange among nestmates is therefore needed to reduce chemical variability among individuals and to integrate environmental compounds into the colony odour. As a result of this process, the referent template is updated during life. This relative plasticity of the recognition system can be exploited by insect social parasites to integrate themselves within the host colonies and to fool host workers about their real identity. By studying the chemical integration strategies of social parasites new insights on the ontogeny of nestmate recognition could be acquired. However, further studies are needed to reveal the neural substrates implicated in learning and memory at different stages of social insect life to better understand how and when template formation occurs.

L. Signorotti · P. d'Ettorre (✉)
Laboratory of Experimental and Comparative Ethology (LEEC),
University of Paris 13, Sorbonne Paris Cité, Villetaneuse, France
e-mail: dettorre@leec.univ-paris13.fr

R. Cervo
Department of Biology, University of Firenze,
Sesto Fiorentino, Italy

L. Aquiloni and E. Tricarico (eds.), *Social Recognition in Invertebrates*,
DOI 10.1007/978-3-319-17599-7_10

Introduction

Recognition plays a central role in parent-offspring interactions, competition, mating and cooperative behaviours such as group defence, brood care, foraging and grooming (e.g., Waldman 1988). Although evidences of recognition abilities in different invertebrate taxa have rapidly accumulated during the past decades (this book), social living certainly generates the most sophisticated and efficient recognition systems. Among invertebrates, insects with eusocial organization represent the most fascinating examples of cooperative group living. Different species of ants, wasps and bees have been traditionally used as model organisms for studying the evolution of cooperative behaviour and recognition systems (Starks 2004). Recognition of group members, i.e., the ability to discriminate between foes and friends, is essential to maintain sociality because it allows altruistic acts to be directed towards related recipients (Hamilton 1987), while excluding competitors and parasites. Differential treatment of relatives and non-relatives, or of different classes of relatives, constitutes kin discrimination. In social insects, colonies typically consist of related individuals, and thus recognition of group membership can act as a proxy for kin recognition (cf. Lenoir et al. 1999). Indeed, no clear evidence of within-colony discrimination based on degree of kin has been provided so far (Boomsma and d'Ettorre 2013).

Here we focus on recognition of group identity (nestmate recognition), the most widespread form of recognition in social insects (d'Ettorre and Lenoir 2010). Group members are usually directly recognized because of traits they express (label) that are perceived by conspecifics and compared with an internal reference (template) stored somewhere in the nervous system. Recognition occurs through the evaluation of how well the label matches the template. This form of identity assessment may be imperfect, leading to acceptance/rejection errors (see Ratnieks 1991), but social insect evolved mechanisms to optimize the system by achieving a unique colony label/template, shared by all colony members, and with minimal overlapping among neighbouring colonies (van Zweden and d'Ettorre 2010). Although we know a great deal about the nature of recognition cues in social insects (which are mainly chemicals, see Fig. 10.1 and this volume Breed et al. and Steiger), we are just starting to understand the perception rules of these nestmate recognition cues and their information processing (Ozaki and Wada-Katsumata 2010; Ozaki and Hefetz 2014). However, relatively little is known about the ontogeny of nestmate recognition, and in particular about the template formation and timing processes. By manipulating individuals' opportunities to interact with conspecifics and/or environment during their life, or part of their life, we may gain a better understanding of the mechanisms underlying nestmate recognition.

Here we present a general overview of the studies that have addressed the ontogeny of nestmate recognition in social hymenoptera, by paying particular attention to the process of template acquisition. Moreover, we will discuss the potential future directions to better understand how recognition information is represented and processed at the peripheral and central level. We begin our overview with highlighting the main general mechanisms that have been proposed to be at the basis of the recognition process.

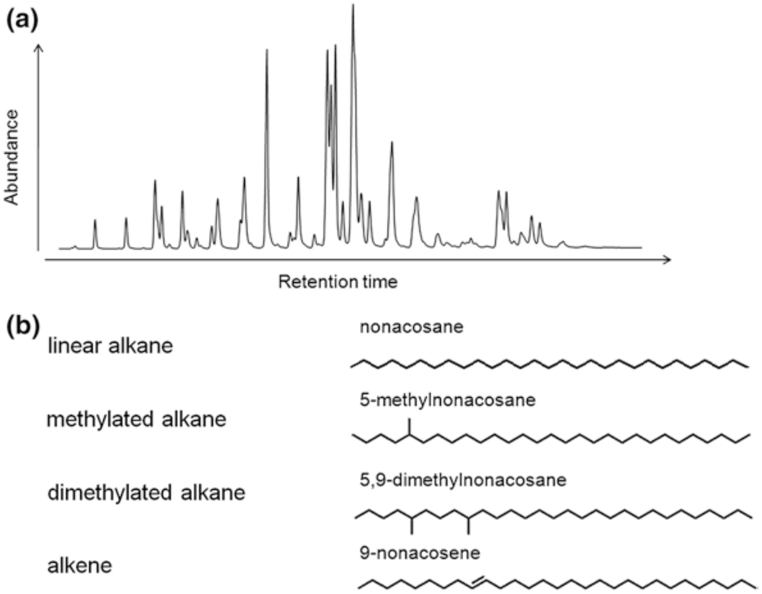


Fig. 10.1 Recognition cues: cuticular hydrocarbons (CHCs) in social insects. **a** Example of chromatogram resulting from CHC analysis by gas chromatography coupled with mass spectrometry (GC-MS). Each *peak* represents one hydrocarbon (or a mixture of few co-eluding hydrocarbons). **b** Examples of the different structural classes of hydrocarbons that can be typically found on the cuticle of social insects. The main structure of hydrocarbons is generally a backbone of carbon atoms with hydrogen atoms attached on empty binding sites. Cuticular hydrocarbons in social insects generally range in size from about 20 to over 40 carbon atoms. CHCs are part of the lipid layer present on the cuticle that protects the insect body against desiccation (Hadley 1994), abrasion and micro-organism infection (Lockey 1988). However, CHCs have assumed a communicative role in several behavioural contexts, especially in social insects where they communicate identity (van Zweden and d'Ettorre 2010; Bruschini et al. 2010). A typical chemical profile of ants, bees and wasps is a complex blend of CHCs, which gives a specific odour to different species and, within a species, to each colony (Singer 1998; Dani 2006; Hefetz 2007; Bruschini et al. 2010; van Zweden and d'Ettorre 2010). There are different classes of hydrocarbons on the cuticle of social insects, although not all of them appear to have the same importance as recognition cues (Châline et al. 2005; Dani 2006; Hefetz 2007; Zweden and d'Ettorre 2010). Methyl-alkanes and alkenes are considered to be relevant nestmate recognition cues (Dani et al. 2001, 2005; Châline et al. 2005; Cervo et al. 2008; Martin et al. 2008; Guerrieri et al. 2009; van Zweden et al. 2010), possibly due to their complex chemical structure compared to linear alkanes, which are more likely involved in water-loss prevention. On the other hand, in the ant *Formica japonica*, all CHC classes appear to be important to achieve discrimination (Akino et al. 2004). The colony odour is generally uniform, but small differences in CHC profiles within the colony can correlated to task (e.g., Greene and Gordon 2003) or caste (Liebig 2010). Moreover, some hydrocarbons, overproduced by queens relative to workers, can act as queen pheromones regulating worker sterility (Peeters et al. 1999; Liebig et al. 2000; Holman et al. 2010, 2013; Monnin 2006; van Oystaeyen et al. 2014)

Recognition Mechanisms

During the last three decades different potential mechanisms underlying recognition of identity have been proposed (reviewed in: d'Ettorre and Lenoir 2010). There is general agreement that these mechanisms are not mutually exclusive or necessary exhaustive, and that their generalization is difficult because ecological constraints and life history trade-offs could affect the recognition mechanism of a particular species (cf. Dreier and d'Ettorre 2009). Generally, recognition could be based on an *indirect* or a *direct* assessment. In the first case recognition is context-based and individuals recognize group members not by their phenotype, but for instance by the specific spatial location where they are encountered. A location, such as the nest site, predictably indicates group membership and all conspecifics encountered therein are recognized as relatives. Alternatively, individuals might recognize group members in a more accurate way, i.e., by *directly* assessing their phenotypic cues through different mechanisms.

Prior association: During social life an individual learns cues from other individuals that are regularly encountered (e.g., group members). These become 'familiar' individuals and in subsequent encounters they will elicit acceptance and/or cooperative behaviour. This type of mechanism requires that each individual must be encountered to become familiar, and thus the recognition process takes place at individual level. There are few examples of individual recognition in social insects, which could be based on this mechanism (Tibbetts 2002; d'Ettorre and Heinze 2005; Dreier et al. 2007; Foubert and Nowbahari 2008). Usually, individual/familiar recognition could work only in small societies, such as those of primitively eusocial wasps (e.g., *Polistes* and Stenogastrinae wasps), in which visual cues are used for the discrimination process (Tibbetts 2002; Baracchi et al. 2013, 2015). On the other hand, ants appear to use chemical cues to achieve individual recognition. For instance, unrelated founding queens of the ant *Pachycondyla villosa* likely use cuticular hydrocarbons (CHCs) to recognize each other individually (d'Ettorre and Heinze 2005).

Phenotype matching: This mechanism allows discrimination of individuals not encountered before. Here, an individual compares the phenotypic cues (label) of the encountered individual with an internal representation (neural template) (Reeve 1989; Crozier and Pamilo 1996; Mateo 2004; d'Ettorre and Lenoir 2010; van Zweden and d'Ettorre 2010). Acceptance/rejection will depend on the similarity/dissimilarity between the template and the label. The template is usually acquired by a learning process. This mechanism is considered as the most used by social insects, being the phenotype (its own or that of nestmates/nest material) a reliable source of cues for recognition of group members (Fig. 10.2).

Recognition alleles (green beard): According to this mechanism, an allele at a single locus (or closely linked genes) should code for three traits linked together: a detectable phenotypic cue (green beard), the ability to recognize this cue and the expression of altruistic behaviour towards individuals with this cue (Hamilton 1964; Dawkins 1976; Holmes and Sherman 1982). In this case, no learning experience is needed.

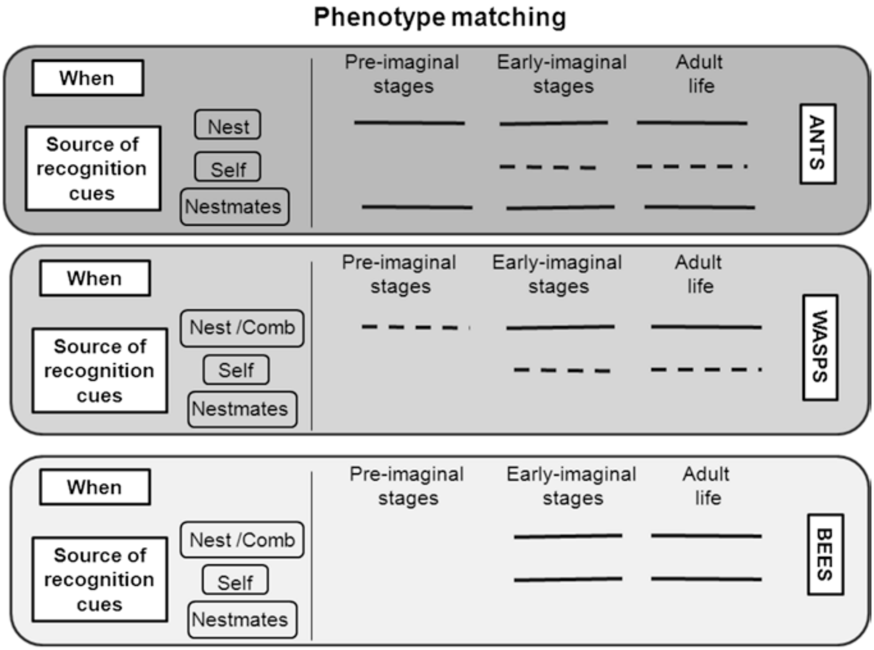


Fig. 10.2 Schematic view of the ontogeny of nestmate recognition ability in ants, wasps and bees according to the phenotype matching model (a possible mechanisms of direct recognition, see text). For each taxonomic group, life stages in which recognition cues can be learned (when) and their source (source of recognition cues) are represented. *Continued lines* indicate factors that have been experimentally shown to play a role in the ontogeny of nestmate recognition, while *dotted lined* indicate factors that are possibly involved

Source of Recognition Cues for Template Formation

In order to build a template, each individual must be in contact with some relevant recognition cues (see Fig. 10.1) during at least part of its life. A parsimonious mechanism for providing all colony members with similar recognition cues could be the exposure to a common source of cues, such as the nest material (Gamboa et al. 1986a). Social wasps of the *Polistes* genus often transfer chemical cues from themselves to the nest material (paper, which easily adsorbs chemical cues) through specific behavioural patterns (Cervo and Turillazzi 1989; Dani et al. 1992; van Hooser et al. 2002). The presence of these cues on the nest surface provides information about colony membership to any new member of the colony (Gamboa et al. 1986a, b). Chemical analyses revealed that the nest material of *Polistes* wasps possesses the same chemical compounds present on the cuticle of the resident wasps (Espelie and Herman 1990; Espelie et al. 1990; Lorenzi 1992; Singer et al. 1992; Cotoneschi et al. 2007). Recognition cues deposition on nest material could thus be important for creating uniformity in the odour label, the so called “Gestalt odour” (cf. Crozier and Dix 1979), and may also contribute to the formation of the referent template. Cues involved in nestmate recognition process are spread within the colony so that nestmates acquire the same or a very similar odour (Crozier and Dix 1979), i.e., a common colony phenotype acting as a uniform identity badge. The *Gestalt* model implies a continuous exchange of recognition cues among nestmates; such mechanism could minimize fluctuation of colonial and individual odours during time due to environmental factors (Carlin and Holldobler 1983; Dahbi and Lenoir 1998; Dahbi et al. 1999; van Zweden et al. 2010). According to the *Gestalt* model, each member of a colony has an odour which is representative of the entire colony. This common odor can thus be used for the formation of the referent template.

There is evidence that some species of *Polistes* wasps learn the referent colony odour (template) from their natal comb early during adult life (Pfennig et al. 1983a, b; Gamboa et al. 1986b; Gamboa 2004; Singer and Espelie 1992). It has been experimentally shown that the presence of the nest material, but not necessarily of nestmates, is important in the ontogeny of nestmate recognition ability in *Polistes fuscatus* wasps (Shellman and Gamboa 1982). *P. fuscatus* gynes (reproductive females) isolated from their natal nest, and gynes exposed only to nestmates after emergence, do not discriminate later between nestmates and unrelated individuals. Similarly, young *Polistes metricus* workers fail to recognize nestmates if they have spent the first four days of their adult life on a comb washed with solvent to remove nest surface compounds (Singer and Espelie 1992). However, in *Polistes dominula* workers, template formation appears to happen in a different way since the absence of nest material (or the presence of alien nest material) during the first four days of adult life does not affect nestmate recognition ability (Signorotti et al. 2014a).

Honeybee guards learn their colony odour from the wax combs in their nest similarly to social wasps (Breed et al. 1995, 1998; d'Ettorre et al. 2006; Couvillon et al. 2007). On the other hand, evidence that nest cues have a recognition function in ants is lacking, although in *Camponotus aethiops* it has been reported that recognition cues can be transferred from one ant to another via the nest soil and this action could affect recognition behaviour (Bos et al. 2011). Ants can leave chemical recognition cues passively on the nest substrate through the contact of their body; however, the resulting deposit is not necessarily colony specific (Lenoir et al. 2009). In ants, template formation appears to be based on cues learned from nestmate workers (e.g., Boulay and Lenoir 2001; Boulay et al. 2003) or from the queen in small colonies (Carlin and Hölldobler 1986). In two *Camponotus* species, there is also evidence that newly eclosed ants familiarize with recognition cues of adult nestmate workers assisting them during eclosion (Morel 1983, 1988). Whatever the source of recognition cues, social insects must be able to identify the common colonial phenotype (e.g., a mix of individual odours to form a single common *Gestalt* odour), perceive it, possibly learn it and form the referent template, on the basis of such phenotype, during a given period of their life.

Timing of Template Formation

Upon emergence, social insects are surrounded by a world of odours that could contain the recognition cues. For the recognition system to be effective, social insects must learn the odour of their specific colony. The role of learning in nestmate recognition is still debated and it remains unclear whether the process of cue learning and template formation is acquired through familiarization during a specific sensitive period (e.g., Jaisson 1987), and when this sensitive period occurs. Indeed, learning could occur at different stages of the insect life (Fig. 10.2).

Early learning: The ability to learn environmental cues during the first moments of life as imago insect (adult) has been investigated since long time. For instance, *Camponotus vagus* and *Formica polyctena* ants develop a preference for a specific habitat as consequence of an early exposure to particular environmental cues, e.g., thyme aroma (Jaisson 1980). In most of the social insect species studied so far, the nestmate recognition cues necessary to build the referent template appear to be learned during the early stages of adult life.

Honeybees learn colonial cues from the wax comb even within an hour after emergence (Breed and Stiller 1992). Studies on the ontogeny of the olfactory nervous system of honeybees have suggested the existence of a critical period, ranging from 3 days before to 4–8 days after emergence, during which the olfactory system appears very flexible in response to environmental changes (Masson et al. 1993). Similarly to honeybees, in *Polistes* wasps early experience after emergence affects nestmate recognition (Gamboa 2004). Gynes of *P. carolina* and *P. fuscatus* isolated at emergence both from their natal nest and their nestmates later failed to recognize nestmates (Pfenning et al. 1983b; Gamboa et al. 1986b). This means that early experience after emergence is crucial for the template development in these species. It has been suggested that the template acquisition in *Polistes* wasps is complete within the first hours after emergence (4 h) (Gamboa 2004); indeed, longer exposure of newly emerged *P. fuscatus* gynes to their natal nest has no effect on discrimination abilities (Pfenning et al. 1983a). *P. fuscatus* wasps are able to remember recognition cues learned during the first hours of adult life up to 20 days later (Pfenning et al. 1983a).

Although numerous evidences suggest that this recognition model is widespread within the genus *Polistes* (including more than 200 species; Carpenter 1996), further investigations are needed since almost all studies were performed on gynes' recognition ability and on limited number of North American species (*P. fuscatus*, Pfenning et al. 1983a; *P. carolina*, Pfenning et al. 1983b; *P. metricus*, Singer and Espelie 1992). Indeed, a recent study conducted on *P. dominula*, an Old World species, suggested the possible implication of other life stages, such as pre-imaginal ones, in which the learning process for the template formation could occur (Signorotti et al. 2014a).

The timing of template formation in ants appears to follow the same general mechanisms as for wasps and bees (Hölldobler and Michener 1980; Jaisson 1991; Lenoir et al. 1999). Early in adult life, each ant learns the colonial cues, which, when encoded as a neural template, serve for colonial membership determination of each encountered individual (Crozier and Pamilo 1996). In *C. vagus* (Morel 1983) and *Camponotus floridanus* (Morel 1988), interactions with older nestmates during the first hours of adult life are necessary to a young worker both to be fully recognized as a nestmate and to develop the ability to recognize nestmates. In some species of ants the recognition of brood can be influenced by the post-eclosion experience (Jaisson 1991). For instance, in *Ectatomma tuberculatum*, an early familiarization of workers with foreign conspecific larvae induces a subsequent preference directed towards them, compared to their own non-familiar larvae (Fénéron and Jaisson 1995). The fact that young workers usually spend the first few days of their life inside the brood chamber may facilitate this learning process (Fénéron and Jaisson 1995).

The use of experimental mixed species groups of ants (rare in nature with the exception of colonies invaded by social parasites) has provided further insight into the timing of template acquisition and its memorization. For instance, newly eclosed workers of *Formica selysi* and *Manica rubida*, reared in artificial mixed colonies, were able to learn allospecific recognition cues, to integrate them into their "colonial template" and to retain them even after one year of separation (Errard 1994a). This implies long-term memory of the template (Errard 1994b), suggesting that the template resides in higher brain centers, such as the mushroom bodies, although, after the long separation, traces of heterospecific hydrocarbons were still present on the cuticle of ants, and could have served as reference (cf. Bos and d'Ettorre 2012).

Pre-imaginal learning: In some ant species, individuals acquire a recognition template for queen recognition (Berton et al. 1991), brood and nestmates recognition (Isingrini et al. 1985; Carlin and Schwartz 1989; Signorotti et al. 2014b) during the pre-imaginal life (i.e., before eclosion). Pre-imaginal olfactory experience affects colony-brood recognition, particularly when experience starts during the first stages of larval development in the ant *Cataglyphis cursor* (Isingrini et al. 1985). Therefore, the first larval instars might be more sensitive to environmental social cues, and/or the total duration of the exposure to the colony odour during pre-imaginal life might affect brood recognition in *C. cursor* adult ants. Similarly, in the ant *Aphaenogaster senilis*, the odour experience during early stages of larval development affects recognition in an adult-adult context (nestmate recognition) (Signorotti et al. 2014b).

Memories from pre-imaginal olfactory experiences can survive after metamorphosis suggesting that the template is probably stored in the higher brain centres. Social insects during their pre-imaginal life are often in contact with recognition cues (nest material/nestmates), therefore the learning process could start during immature stages, when the olfactory system is being formed. Very little is known about structural modifications of social insects' brain during development

(Gronenberg et al. 1996; Farris et al. 1999). The mushroom bodies (higher brain centres) are involved in higher associative functions (learning and memory) and play a key role in the neuronal control of adaptive behavioural modifications and in the processing and storage of chemosensory information (Erber et al. 1980; Menzel 1993; Heisenberg 1994). Certain brain structures, such as the mushroom bodies, develop during larval life (Farris et al. 1999). Indeed, studies on adult mushroom bodies in *Apis mellifera* showed that there are no signs of cell proliferation (neurogenesis) after pupation (Fahrbach et al. 1995; Cayre et al. 1996). Similarly, in the ant *C. floridanus*, neurogenesis is complete in young pupae and no new Kenyon cells (intrinsic neurons of the mushroom bodies), that might contribute to mushroom bodies growth, are produced in adults. Thus, the increase of mushroom bodies' volume in adults is most likely the result of an outgrowth of existing neurons (Gronenberg et al. 1996). The connection between pre-imaginal experience and adult behaviours could be a consequence of the survival of larval/pupal neurons during metamorphosis in the higher brain centres, enabling the persistence of memories formed during pre-imaginal stages in the adult brain (Tully et al. 1994; Lee et al. 1999; Ray 1999).

There are no specific studies on pre-imaginal learning of nestmate recognition cues in social wasps, although some insight comes from studies on facultative social parasites (Lorenzi et al. 2007, 2011; Costanzi et al. 2013). Usually, *Polistes* dominant female performs a typical abdomen stroking behaviour over the nest surface to possibly release chemical cues on the comb, thus spreading her own odour (Dani et al. 1992; van Hooser et al. 2002; Dapporto et al. 2007). Wasp social parasites also perform this behaviour after invading the host nest (Cervo and Turillazzi 1989; Zacchi et al. 1996; Turillazzi et al. 2000). Costanzi et al. (2013) suggested that *P. dominula* workers could memorize the colony odour experienced during pre-imaginal development. They performed an experiment in which natural nests of *P. dominula* wasps were divided into two parts and brood emerged either in the part marked by their genetic mothers or in the part overmarked by *Polistes nimphus* usurpers, in absence of adults. *P. dominula* workers emerged in usurped nests accepted both their usurper and their genetic mother, suggesting that they could have learned their mother's odour during pre-imaginal life. Moreover, worker discrimination abilities were lowest in colonies where the odour changes due to usurpation were largest, indicating a possible process of comparison between the previously learned odour and the new one, i.e., the odour of the parasite (Costanzi et al. 2013). The occurrence of pre-imaginal learning for template formation in *P. dominula* wasps has been recently proposed also by us (Signorotti et al. 2014a). We showed that workers, taken from their natal comb when the natural emergence occurs, displayed correct discrimination abilities at the age of five days, regardless of their olfactory experience during the first four days of adult life. Ecological pressures might have led to the evolution of an advantageous precocious cues learning in *P. dominula* wasps (Signorotti et al. 2014a), a species characterized by high rate of inter- and intraspecific social parasitism (Cervo 2006).

In the Stenogastrinae wasp *Liostenogaster flavolineata*, chemicals on the nest material are scarce since the comb is made with mud; however, in this species an abdominal substance secreted by the Dufour's gland, rich of the same compounds as the wasp cuticle (Cervo et al. 2002; Keegans et al. 1993), is transferred directly on eggs and small larvae (Turillazzi 1985). Although this secretion could contain suitable cues for the acquisition of the recognition template during pre-imaginal stages, behavioural experiments did not confirm the use of this abdominal substance for the formation of the template (Cervo et al. 2002; Turillazzi et al. 2008). Further studies on different species are needed to clarify the possible implication of pre-imaginal learning in template formation.

Template updating during adult life: The occurrence of early and/or pre-imaginal template formation does not exclude a subsequent template updating during adult life. Individual odour and thus colonial odour are dynamic and change over time (Vander Meer and Morel 1998; Lahav et al. 2001; Sledge et al. 2004; Dapporto et al. 2005; van Zweden et al. 2009; Newey et al. 2009; Sturgis and Gordon 2012), suggesting that the template should be updated throughout the adult life for an effective recognition system to be maintained (Liu et al. 1998). We have direct evidences that in several species of Myrmicinae, Formicinae and Ponerinae ants, workers exchange recognition cues (Vienne et al. 1995; Meskali et al. 1995; Soroker et al. 1995, 1998; Dahbi et al. 1999; Boulay et al. 2000; van Zweden et al. 2010) allowing the formation of a unique colonial odour; therefore workers need frequent social contacts with nestmates to maintain an accurate referent template reflecting the current shared odour. In the ant *Camponotus fellah*, the isolation of adult workers for 20 days from the colonial cues can partially erase the workers' template, leading to errors in nestmate recognition due to the impossibility to update the template (Boulay and Lenoir 2001). Social contact during adult life appears to be necessary to maintain a referent template and thus the capacity to discriminate between aliens and nestmates.

Studies with artificial mixed-species groups provided further insight regarding cue-exchange among colony members and the template formation using "collective" nestmate recognition compounds (Stuart 1988; Errard et al. 2006). Ant workers reared in mixed-species groups learn and memorize the homo- and heterospecific chemical cues (i.e., mixed colonial odour) and they incorporate them into their recognition template (Errard 1994b). This template reformation, on the basis of the presence of heterospecific cues into the colonial odour, likely allows the cohabitation of two species in the same nest without displaying interspecific aggression (Vienne et al. 1990; Errard 1994a). Two hypotheses have been suggested (Errard 1994b) to explain the tolerance between two different cohabiting species in mixed colonies: (1) workers could learn two different recognition template (homo- and heterospecific); or (2) workers could compare during each encounter the chemical cues exhibited by the encountered individual with its own chemical profile that possesses heterospecific cues.

Even though no direct evidences for a template updating process are available for social wasps, some information comes again from studies on social parasitism in *Polistes* wasps and indirectly indicates a similar process of updating. For instance, *Polistes biglumis* wasps recognize only the odour of their species in non-parasitized colonies, but learn a template that fits the odour of their own species and that of the social parasite, *Polistes atrimandibularis*, in parasitized colonies (Lorenzi et al. 1999). The process of template updating has also been shown in *Apis mellifera*: guard bees change their referent template after a unidirectional combs transfer from a 'donor' hive to a 'receiver' hive. Couvillon et al. (2007) suggested that the wax comb transfer increases the acceptance of non-nestmates belonging to the 'comb donor' not by changing the odour of the bees, but by updating their colony odour template directly from the wax comb rather than from the contact with conspecifics.

Individual Acquisition of Colonial Cues

Several strong evidences indicate that CHCs are involved in nestmate recognition in social insects (see Fig. 10.1). A particular CHC blend provides the label to each individual, which reveals colony membership. Young individuals produce their own CHCs (genetic components) and later adsorb colonial cues from nestmates or surrounding environment (environmental components) (Vander Meer and Morel 1998; van Zweden et al. 2009), in order to achieve a chemical integration by developing a *Gestalt* odour (Dahbi et al. 1998; Lenoir et al. 1999). Indeed, newly eclosed social insects appear to be "chemically insignificant", i.e., they have only low amounts of CHCs. This allows acceptance of newly eclosed individuals in foreign colonies (Stuart 1992; Lenoir et al. 1999; Breed et al. 2004; Lorenzi et al. 2004; Mitra et al. 2014), since the total quantity of the CHCs on their cuticle is probably below the quantitative perceptual threshold for nestmate recognition (Cini et al. 2009; Ichinoise and Lenoir 2010; Cappa et al. 2014). The acceptance threshold may shift in an adaptive way according to environmental conditions (e.g., Downs and Ratnieks 2000), although how this behavioral shift relates to the underlying perceptual mechanisms is not known.

Newly emerged honeybees gain tolerance inside their colony by presenting the so-called "blank state", i.e., fewer total quantity of chemicals on the cuticular surface than older bees (Breed et al. 2004). *P. fuscatus* adult wasps do not discriminate between nestmate and non-nestmate young gynes (less 48 h-old). Indeed, these young gynes show a slightly quantitatively different chemical profile than 72 h-old gynes, which are instead well recognized (Gamboa et al. 1986b; Panek et al. 2001). It has been shown that *P. fuscatus* and *P. dominula* young wasps change significantly their CHC blend between 24 and 72 h particularly in respect of abundance, relative abundance, and colony specificity of compounds (Panek et al. 2001; Lorenzi et al. 2004). In *P. dominula* wasps, the percentage of certain hydrocarbon classes in the profile decrease significantly during the first 72 h after emergence together with the increase of other hydrocarbon classes. This suggests that certain CHCs may be more important for recognition in younger *Polistes* wasps and/or newborns are recognized by adults as a group with a specific collective profile (Lorenzi et al. 2004).

Likewise, recognition cues of newly emerged bees are consistent across colonies. This suggests that newly emerged bees could have a typical profile that may serve as a cue to older bees for recognizing the newly emerged bee's status (Breed et al. 2004). Laboratory reared *A. mellifera* younger than 12 h are accepted in alien conspecific nests, but acceptance rapidly declines when introduced bees are older (Breed et al. 1988). In many ant species, newly eclosed workers are readily adopted by an unrelated colony (Jaisson 1991). In the ant, *Camponotus pennsylvanicus*, the acceptance of young workers in alien conspecific nests is maximal during the first hours after birth and gradually decreases from 5–8 days after eclosion (Carlin and Hölldobler 1986). Adult *C. cursor* workers are accepted in alien colonies if 4 days old or younger (Nowbahari and Lenoir 1989). However, this is not always the case. In three North American species of *Leptothorax* ants, the transfer of workers 8 months after birth between groups originating from the same colony caused very little aggression (Stuart 1987a). It has also been suggested that young workers might be highly acceptable in alien colonies because they produce an attractive secretion that inhibits the aggression of older workers (Jaisson 1972), but chemical data supporting this hypothesis are still lacking. Callow workers of the slave-making ant *Polyergus rufescens* appear to emit a secretion that is very attractive for *Formica* host workers; they excrete fluid droplets from the tip of the gaster and *Formica* workers actively lick these secretions (proctodeal trophallaxis). This fluid might act as an appeasement signal facilitating the adoption of the slave makers (d'Ettorre and Errard 1999).

Overcoming the Recognition System: Social Parasites

The recognition system as well as its constituent parts (template and label-CHCs) is flexible. As explained above, individual recognition cues can change over time due to environmental factors, and thus the referent template needs to be updated accordingly. This flexibility can be exploited by social parasites to infiltrate the host colonies. The study of parasite strategies to overwhelm the host colony's defence gives the opportunity to better understand the mechanisms at the basis of nestmate recognition process.

Insect social parasites use the social system of other species to exploit the colony worker-force over an extended period of time so that host workers rear parasite reproductives (Wilson 1971). The first problem the parasite has to solve is to be accepted into the host colony as nestmate. One strategy, named "chemical insignificance" (also "blank state"), is to possess a weak quantity of labels on the cuticle that allows the parasite being undetected by the host (Lenoir et al. 2001). For instance, *Acromyrmex insinuator*, social parasite of the leaf-cutting ant *Acromyrmex echinatior*, appears to adopt this strategy: even if they show remarkably different cuticular hydrocarbon profiles compared to the host, they possess a lower total amount of compounds, which are possibly not perceived by the hosts (Lambardi et al. 2007). Such feature, present in most of newly emerged social insects, could represent an effective strategy employed by the parasites to usurp host colonies. An "insignificant status" could allow parasites to initially gain entrance into a host colony, before achieving chemical integration (Lenoir et al. 2001). Two other strategies are possible to reach some degree of chemical congruency with the host: chemical mimicry (in which the parasite actively biosynthesizes the host cues) or camouflage (in which the parasite gets the cues from the host both by passive acquisition, i.e., via contact with host and nest material, and by active acquisition, i.e., via allogrooming and trophallaxis) (Dettner and Liepert 1994; Lenoir et al. 2001). Before usurpation of a *P. dominula* nest, females of the obligate social parasite *Polistes sulcifer* have a chemical profile both simpler and different from that of the host species. A chemical integration process to match the host odour occurs as soon as 90 min after usurpation (Turillazzi et al. 2000). Similarly, chemical analysis of *P. rufescens* ant parasites and its host species revealed that the newly hatched slaver-markers lack a chemical signature at emergence but later develop or acquire a chemical profile matching that of the host species present in the nest (d'Ettorre et al. 2002). Queens of *Polyergus breviceps* and *P. rufescens* fatally attack the resident queen of their *Formica* host species and, during aggressive interactions, cuticular compounds from the host queen are possibly transferred to the parasite queen (Johnson et al. 2001; Lenoir et al. 2001). Parasites often exhibit behaviours involving physical contacts with both the nest surface and their hosts, which may facilitate the mutual transfer of cuticular chemicals (Turillazzi et al. 1990; Lenoir et al. 1992, 2001 Cervo and Dani 1996; Errard et al. 1997; Cervo 2006).

Although the parasite's chemical integration strategies are fundamental during colony invasion, it is possible that chemical host-parasite congruency is not fully achieved at this stage. Therefore, host acceptance could later be improved by modifying the host's referent template. If the host workers, emerging in parasitized colonies, find a good match between the template (referent colonial chemical profile) and the parasite's odour, the parasite will be recognized as nestmate. Indeed, as outlined above, early experiences can be crucially important for the development of the recognition template. Social parasites can exploit early experiences of their hosts by intervening at the right time. For example, slave-making ants during raids usually pillage host pupae so that new host workers will emerge in a colony containing the slave-makers' odour on which they will form the template. This appears to be an effective strategy, indeed, among the ten ant genera displaying interspecific slavery, only one is known to form slave-maker colonies resulting from the mix with adult host workers (Hölldobler and Wilson 1990). Early experience with the odour of parasites in *Temnothorax unifasciatus* ants, the principal host species of *Chalepoxenus muellerianus* and *Myrmoxenus ravouxi* slave-makers, affects nestmate discrimination ability and the successful enslavement by two slave-maker species. However, this is not the case of *Temnothorax parvulus*, a species that in nature is never parasitized. This could be due to a genetically based system of odour discrimination or to an earlier sensitive period for the template formation, namely the pre-imaginal stages (Blatrix and Sermage 2005).

Nestmate discrimination has been shown to be less influenced by social environment during early stages in the ant genus *Camponotus* than in the genus *Formica* (Carlin et al. 1987). Interestingly, no species of *Camponotus* is parasitized by slave-makers, while many *Formica* species are regular hosts to slave-makers. Early behavioural plasticity could thus facilitate the evolution of parasitism. Coevolution occurs between parasites and their hosts (Foitzik et al. 2001; Hare and Alloway 2001) and hosts and parasites species usually show similar cuticular hydrocarbon profiles (Kaib et al. 1993; Brandt et al. 2005), which might facilitate learning of the parasite profile by the host species. Slave-making *P. rufescens* workers are able to adopt a different cuticular signature, both qualitatively and quantitatively, when reared by different *Formica* hosts species as a result of certain plasticity; however, when reared in isolation they show higher chemical similarities with their primary host *F. cunicularia* (d'Ettorre et al. 2002). This similarity could promote the formation of the host template based on the odour of the parasite. In parasitized wasp colonies, the hosts' early experience is also important for the parasite acceptance. Wasp social parasites normally usurp the host nest before emergence of the first generation of workers (Cervo 2006), thus having the opportunity to manipulate the colony odour in absence of workers. This process could allow both the usurpers and their future brood to be recognized as nestmates. Young *P. atrimandibularis* parasites already possess the specific compounds that allow discrimination in *P. biglumis* non-parasitized colonies, however, they are accepted in parasitized nests because of the incorporation of the parasite-specific components in the referent template of the host species (Lorenzi et al. 1999). Parasites could manipulate colony odours by supplementing with their specific compounds the nest material on which the hosts likely form the template (Lorenzi and Bagnères 1996; Lorenzi et al. 1996; Turillazzi et al. 2000).

Social insects' referent template must be flexible to incorporate all the changes of colonial recognition cues due to the environmental factors, for instance to avoid rejection errors (rejection of nestmates). Yet, this plasticity represents a weakness of the recognition system because the parasites can be part of the environmental factors that cause fluctuations of recognition labels (by depositing their own cues and rearing their own brood). Moreover, parasites developing strategies to mask themselves as nestmates, are more easily accepted. In a cost–benefit balance the host should accept the parasites if the costs of correct discrimination exceed the benefits (Zahavi 1977) because recognition errors in which nestmates would be rejected are very costly.

Concluding Remarks and Future Directions

Social insects have been largely used as models for studying detection, perception, learning and memory of recognition cues through the manipulation of their olfactory experiences and their consequent behavioural responses. Workers in a colony gather experience during their whole life, and almost all behavioural responses are fine-tuned through learning (cf. Jeanson and Weidenmüller 2013). Despite this, some fundamental aspects of nestmate recognition system, such as the timing of template formation and its neural location, remain to be clarified.

Self-Referent Phenotype Matching for Recognition

During the last decades, studies on the ontogeny of nestmate recognition have revealed the presence of a sensitive period for learning, during which the template for the colony odour is formed. Social insects appear to learn the crucial recognition cues (heritable, environmental or both) during a sensitive temporal window after birth (early learning) and then use them as referent according to a phenotype matching process. However, they could also use their own phenotypes as referent for nestmate recognition and theoretically this would be the most accurate way to assess relatedness (Mateo 2004). Self-referencing might turn out to be the mechanism of recognition in several contexts that had previously been thought to depend solely on genetic (innate) cues (Jutsum et al. 1979; Getz and Smith 1983; Mintzer and Vinson 1985; Breed et al. 1985; Stuart 1987b). Nevertheless, in the case of social insects, self-referencing could lead to evaluation problems. First, the individuals of a colony usually show differences, although small, in their chemical profile and so every slightly "different" nestmates could be rejected. Indeed, optimal acceptance thresholds theory predicts when an individual should accept or reject in a given encounter, despite incurring the double costs of errors in rejecting true nestmates and accepting alien individuals (Reeve 1989; Johnson et al. 2011). Second, phenotypes used for self-referencing are themselves malleable constructs because CHCs can be subjected to changes due to environmental factors and/or the physiology of the individuals (Wagner et al. 1998; Nielsen et al. 1999; Buczkowski et al. 2005; Provost et al. 2008). Third, in multiple paternity or maternity systems, this process of learning and discrimination could favour nepotistic behaviours and thus it would not be advantageous in ants, bees and wasp societies where such mating systems can be present (Boomsma and d'Ettorre 2013).

Self-referent phenotype matching could be favoured when there is a high risk to learn from foes, such as social parasites. Living in different habitats and under different ecological pressures (e.g., social parasitism) could promote the development of recognition systems with different characteristics. Few studies have reported self-matching in eusocial hymenoptera (Page and Breed 1987; Michener and Smith 1987). Other sources of recognition cues appear to be important in the template acquisition process, such as experience with nest material (Gamboa 2004) or nestmates (Jaisson 1991; Lenoir et al. 1999) during the early stages of life. However, an individual can never be separated from self-cues. Exclusion of self-referencing in *P. fuscatus* gynes was supported by the fact that individuals isolated from eclosion were not able to develop correct recognition ability but were recognized by the adults. This suggests that the recognition cues were present on the young gynes' body but were not used by them to form the referent template (Gamboa et al. 1986b). However, *P. dominula* workers reared in isolation (without nestmates or nest material) for four days from birth are able to perform correct discrimination between nestmates and non-nestmates (Signorotti et al. 2014a), suggesting the possible occurrence of self-referencing for template formation during the first days of life, at least in this species.

Learning cues from self during the first hours of adult life implies that such recognition cues are already present and perceptible. However, most of the studies report that newly eclosed individuals possess low amounts of recognition cues (see above). More studies are needed to investigate whether the amount of CHCs present on young individuals is over the perception thresholds (cf. Cini et al. 2009; Ichinose and Lenoir 2010; Cappa et al. 2014). Evidence for self-referent phenotype matching in honeybees (Getz and Smith 1983, 1986) has been criticized due to the difficulty of entirely eliminating pre-imaginal and social learning. Futures studies manipulating the breeding environment are needed to elucidate whether self-referent phenotype matching occurs in social insects.

Pre-imaginal Learning and the Neural Machinery at the Basis

Despite prenatal olfactory learning has been demonstrated in a wide variety of animals (Hepper and Waldman 1992; Hudson 1993; Schaal et al. 2000; Hepper 2003; Caubet et al. 1992), the possible importance of learning during immature life in the ontogeny of recognition abilities and social memories has been neglected so far in social insects. The ability of individuals to learn prenatally may be of particular importance in the development of social recognition by ensuring that individuals learn about genetically related conspecifics (Hepper 1987; Robinson and Smotherman 1991). There is evidence that pre-imaginal experience affects recognition abilities in Myrmicinae (Signorotti et al. 2014b) and Formicinae (Isingrini et al. 1985; Carlin and Schwartz 1989) ants. This means that some important information could be processed during the larval stages, retained across the pupal stage, and then integrated into the adult nervous system. Adults and larvae of holometabolous insects are morphologically divergent, reflecting their different lifestyles. Metamorphosis could imply dramatic changes in larval organization, including replacement of the integument and many other tissues, and histolysis of almost all muscles. However, radical changes in neuronal design from the larval to the adult system is not very likely, given that the metamorphosis of the nervous system is largely parsimonious (Tissot and Stocker 2000). Persistence of neurons is not only economic in terms of minimal numbers of neurons to be formed, but might also be crucial for complex metamorphic processes such as axon guidance or memory retention (Tissot and Stocker 2000). Most of the studies on larval chemosensory system have been conducted using *Drosophila* as model (Singh and Singh 1984; Ito and Hotta 1992; Heimbeck et al. 1999; Lee et al. 1999). The larval olfactory circuit of *Drosophila* shows a strong overall similarity to the adult design, but it is organized in a numerically much reduced and almost completely non-redundant way (Ramaekers et al. 2005; Python and Stocker 2002). Young individual neurons could possess integrative capacities as high as that of their adult counterparts; indeed, larvae already exhibit appetitive olfactory learning that relies on a small subset of embryonic-born Kenyon cells (Cobb and Domain 2000; Pauls et al. 2010). Very little is known about the development of larval chemosensory system in social insects.

To elucidate unexplored phenomena, such as pre-imaginal learning, it is essential to determine the actual cognitive load of this particular process and identify how many neurons, connections, and sequential stages of information processing are required to form stable memories until the adult age. From the experimental point of view, one of the major problems in studying pre-imaginal learning lays in the difficulty to assess the behaviour of individuals just after emergence (in most cases they will not respond because too young), and thus there might always be a component due to early learning during the first phase of adult life. Moreover, it could be hard to differentiate between pre-imaginal and self-referent learning if some recognition cues are transferred from the pupal to the adult stage (see Corbet 1985 for discussion on the “chemical legacy hypothesis”). Although recognition cue exchange is possible between adult-adult or adult-nest material (Soroker et al. 1994, 2003; Dahbi et al. 1999; Breed et al. 1995), we do not know whether the larval-adult cue-transfer is possible in social insects.

Regardless of the cue-source, sensitive periods are reflected in behaviour but they are actually a property of neural circuits: behavioural responses are not possible without the processing of the information in the neural machinery. We think that much needs to be learned about nervous system development, neuronal plasticity and the adaptation by studying the brain of social insects. For instance, there are no studies on olfactory organ and receptor cells in ants, bees or wasp larvae.

The Neural Substrates for Nestmate Recognition

Memory has an important role in the discrimination process, both in pre-imaginal and early learning. Several species of ants and paper wasps show long-term memory of nestmate cues, even after overwintering, and there are some evidences that their templates, formed through an imprinting-like process, are maintained over time (Ross and Gamboa 1981; Pfennig et al. 1983b; Gamboa 1988; Jaisson 1991; Errard 1994b; but see Dapporto et al. 2004). However, some characteristics of the recognition system (see above) suggest that the template is not as stable as previously thought and that it could be reformed during life (template updating). It is largely accepted that the neural substrates of memories are parts of the higher brain centers such as mushroom bodies and/or lateral horn (d'Ettorre and Lenoir 2010; Bos and d'Ettorre 2012), but how do they contribute to the behavioural plasticity is less well understood (Heisenberg 1998).

Template updating may result from the formation of new memories each time the referent colonial odour changes or from sensory adaptation or habituation processes, thus the template could be decentralized. In *Camponotus japonicus* ants, the olfactory *sensilla* have been proposed as processing organs for nestmate recognition cues (Ozaki et al. 2005). These *sensilla* show a physiological activity only if exposed to CHCs of non-nestmates, suggesting sensory adaptation as proximate mechanism of nestmate recognition due to the permanent exposure to the colonial odours. However, there are neurophysiological evidences that, for instance in *C. floridanus* ants, colony odours from both nestmates and non-nestmates are perceived and produce a response in the antennal lobes, the first-order integration centers of the central nervous system, contradicting the sensory adaptation hypothesis for nestmate recognition (Brandstaetter et al. 2011). The template reformation is a relatively slow process, taking several hours (Leonhardt et al. 2007; Stroeymeyt et al. 2010) while sensory adaptation at antennal level is much faster. Template adjustment could probably not reverse immediately the own colonial template previously learned (Leonhardt et al. 2007; Harano and Sasaki 2006). During the early phase of template renewal, old memories could be useful to avoid recognition errors while the colony odour is changing. Even if memory is costly (Guerrieri et al. 2011), it could play a key role in the discrimination process. Habituation and/or sensory adaptation, being less costly, could partly replace the use of long-term memory to discriminate nestmates and could be useful during template updating, but the use of memories from the pre-imaginal and/or early adult stages of life remain a key feature in the ontogeny of recognition. A fundamental debate that continues to the present is whether specific mechanisms underlie sensitive periods for learning recognition cues, or whether the presence of sensitive periods is a natural consequence of functional brain development. Future integrated studies are needed to establish how social insect brains develop to allow the complex communication signals to be generated and processed, enlightening certain unclear phenomena such as pre-imaginal learning.

References

Akino T, Yamamura K, Wakamura S, Yamaoka R (2004) Direct behavioral evidence for hydrocarbons as nestmate recognition cues in *Formica japonica* (Hymenoptera: Formicidae). Appl Entomol Zool 39:381–387

Baracchi D, Petrocelli I, Cusseau G, Pizzocaro L, Teseo S, Turillazzi S (2013) Facial markings in the hover wasps: quality signals and familiar recognition cues in two species of Stenogastrinae. Anim Behav 85(1):203–212

Baracchi D, Petrocelli I, Chittka L, Ricciardi G, Turillazzi S (2015) Speed and accuracy in nestmate recognition: a hover wasp prioritizes face recognition over colony odour cues to minimize intrusion by outsiders. Proc R Soc B 282(1802):2014–2750

Blatrix R, Sermage C (2005) Role of early experience in ant enslavement: a comparative analysis of a host and a non-host species. Fron Zool 2(1):13

Berton F, Lenoir A, Nowbahari E, Barreau S (1991) Ontogeny of queen attraction to workers in the ant *Cataglyphis cursor* (Hymenoptera: Formicidae). Insect Soc 38:293–305

Boomsma JJ, d'Ettorre P (2013) Nice to kin and nasty to non-kin: revisiting Hamilton's early insights on eusociality. Biol Lett 9(6):20130444

Bos N, d'Ettorre P (2012) Recognition of social identity in ants. Front Psychol 3:83

Bos N, Grinsted L, Holman L (2011) Wax on, wax off: nest soil facilitates in direct transfer of recognition cues between ant nestmates. PLoSONE 6:e19435

Boulay R, Lenoir A (2001) Social isolation of mature workers affects nestmate recognition in the ant *Camponotus fellah*. Behav Process 55:67–73

Boulay R, Hefetz H, Soroker V, Lenoir A (2000) *Camponotus fellah* colony integration: worker individuality necessitates frequent hydrocarbon exchanges. Anim Behav 59:1127–1133

Boulay R, Katzav-Gozansky T, Vander Meer RK, Hefetz A (2003) Colony insularity through queen control on worker social motivation in ants. Proc R Soc Lond B 270:971–977

Brandstaetter AS, Rössler W, Kleineidam CJ (2011) Friends and foes from an ant brain's point of view—neuronal correlates of colony odors in a social insect. PLoS ONE 6(6):e21383

Brandt M, Heinze J, Schmitt T, Foitzik S (2005) A chemical level in the coevolutionary arms race between an ant social parasite and its hosts. J Evol Biol 18:576–586

Breed MD, Stiller TM (1992) Honey bee, *Apis mellifera*, nestmate discrimination: hydrocarbons effects and the evolutionary implications of comb choice. Anim Behav 43:875–883

Breed MD, Butler L, Stiller TM (1985) Kin discrimination by workers in genetically mixed groups. Proc Natl Acad Sci USA 82:3058–3061

Breed MD, Stiller TM, Moor MJ (1988) The ontogeny of kin discrimination cues in the honey bee, *Apis mellifera*. Behav Genet 18(4):439–448

Breed MD, Garry MF, Pearce AN, Bjostad L, Hibbard B, Page RE (1995) The role of wax comb in honeybee nestmate recognition: genetic effects on comb discrimination, acquisition of comb cues by bees, and passage of cues among individuals. Anim Behav 50:489–496

Breed MD, Leger EA, Pearce AN, Wang YJ (1998) Comb wax effects on the ontogeny of honey bee nestmate recognition. Anim Behav 55:13–20

Breed MD, Perry S, Bjostad LB (2004) Testing the blank state hypothesis: why honey bee colonies accept young bees Insect Soc 51:12–16

Bruschini C, Cervo R, Turillazzi S (2010) Pheromones in social wasps. In: Litwack G (ed) Vitamins and hormones, vol 83. Academic Press, Burlington, pp 447–492

Buczkowski G, Kumar R, Suib SL, Silverman J (2005) Diet-related modification of cuticular hydrocarbon profiles of the Argentine ant, *Linepithema humile*, diminishes intercolony aggression. J Chem Ecol 31: 829–843

Cappa F, Bruschini C, Cipollini M, Pieraccini G, Cervo R (2014) Sensing the intruder: a quantitative threshold for recognition cues perception in honeybees. Naturwiss 101:149–152

Carlin N, Hölldobler B (1983) Nestmate and kin recognition in interspecific mixed colonies of ants. Science 222:1027–1029

Carlin N, Hölldobler B (1986) The kin recognition system of carpenter ants (*Camponotus* spp.). I. Hierarchical cues in small colonies. Behav Ecol Sociobiol 19:123–134

Carlin NF, Schwartz PH (1989) Pre-imaginal experience and nestmate brood recognition in the carpenter ant, *Camponotus floridanus*. Anim Behav 38:89–95

Carlin NF, Halpern R, Hölldobler B, Schwartz P (1987) Early learning and the recognition of conspecific cocoons by carpenter ants (*Camponotus* spp.). Ethology 75:306–316

Carpenter JM (1996) Phylogeny and biogeography. In: Turillazzi S, West-Eberhard MJ (eds) Natural history and evolution of paper wasps. Oxford University Press, Oxford, pp 18–57

Caubet Y, Jaisson P, Lenoir A (1992) Preimaginal induction of adult behaviour in insects. Q J Exp Psychol B 44B:165–178

Cayre M, Strambi C, Charpin P, Augier R, Meyer MR, Edwards JS, Strambi A (1996) Neurogenesis in adult insect mushroom bodies. J Comp Neurol 371:300–331

Cervo R (2006) *Polistes* wasps and their social parasites: an overview. Ann Zool Fenn 43:550–563

Cervo R, Dani FR (1996) Social parasitism and its evolution in *Polistes*. In: Turillazzi S, West Eberhard MJ (eds) Natural history and the evolution of paper wasps. Oxford University Press, Oxford, pp 98–112

Cervo R, Turillazzi S (1989) Nest exchange experiments in *Polistes gallicus* (L.) (Hymenoptera Vespidae). Ethol Ecol Evol 1(2): 185–193

Cervo R, Dani FR, Zanetti P, Massolo A, Turillazzi S (2002) Chemical nestmate recognition in a stenogastrine wasp, *Liostenogaster flavolineata* (Hymenoptera: Vespidae). Ethol Ecol Evol 14:351–363

Cervo R, Dani FR, Cotoneschi C, Scala C, Lotti I, Strassmann JE, Queller DC, Turillazzi S (2008) Why are larvae of the social parasite wasp *Polistes sulcifer* not removed from the host nest? Behav Ecol Sociobiol 62(8):1319–1331

Châline N, Sandoz JC, Martin SJ, Ratnieks FLW, Jones GR (2005) Learning and discrimination of individual cuticular hydrocarbons by honeybees (*Apis mellifera*). Chem Senses 30:327–335

Cini A, Gioli L, Cervo R (2009) A quantitative threshold for nestmate recognition in a paper social wasp. Biol Lett 5:459–461

Cobb M, Domain I (2000) Olfactory learning in individually assayed *Drosophila* larvae. Proc R Soc Lond B 267:2119–2125

Corbet SA (1985) Insect Chemosensory Responses—a chemical legacy hypothesis. Ecol Entomol 10(2):143–153

Costanzi E, Bagnères AG, Lorenzi MC (2013) Changes in the hydrocarbon proportions of colony odor and their consequences on nestmate recognition in social wasps. PLoS ONE 8(5):e65107

Cotoneschi C, Dani FR, Cervo R, Sledge MF, Turillazzi S (2007) *Polistes dominulus* (Hymenoptera: Vespidae) larvae have their own chemical signatures. J Insect Physiol 53:954–963

Couvillon MJ, Caple JP, Endsor SL, Kärcher M, Russell TE, Storey DE, Ratnieks FLW (2007) Nest-mate recognition template of guard honeybees (*Apis mellifera)* is modified by wax comb transfer. Biol Lett 3:228–230

Crozier RH, Dix MW (1979) Analysis of two genetic models for the innate components of colony odor in social Hymenoptera. Behav Ecol Sociobiol 47:217–224

Crozier RH, Pamilo P (1996) Evolution of social insect colonies. Oxford University Press, Oxford

Dahbi A, Lenoir A (1998) Nest separation and the dynamics of the Gestalt odor in the polydomous ant *Cataglyphis iberica* (Hymenoptera, Formicidae). Behav Ecol Sociobiol 42:349–355

Dahbi A, Cerdá X, Lenoir A (1998) Ontogeny of colonial hydrocarbon label in callow workers of the ant *Cataglyphis iberica*. Comptes Rendus de l'Académie des Sciences—Series III—Sciences de la Vie 321:395–402

Dahbi A, Hefetz A, Cerdá X, Lenoir A (1999) Trophallaxis mediates uniformity of colony odor in *Cataglyphis iberica* ants (Hymenoptera, Formicidae). J Insect Behav 12:559–567

Dani FR (2006) Cuticular lipids as semiochemicals in paper wasps and other social insects. Ann Zool Fenn 43:500–514

Dani FR, Cervo R, Turillazzi S (1992) Abdomen stroking behaviour and its possible functions in *Polistes dominulus* (Christ) (Hymenoptera Vespidae). Behav Process 28:51–58

Dani FR, Jones GR, Destri S, Spencer SH, Turillazzi S (2001) Deciphering the recognition signature within the cuticular chemical profile of paper wasps. Anim Behav 62:165–171

Dani FR, Jones GR, Corsi S, Beard R, Pradella D, Turillazzi S (2005) Nestmate recognition cues in the honey bee: differential importance of cuticular alkanes and alkenes. Chem Senses 30:477–489

Dapporto L, Pansolli C, Turillazzi S (2004) Hibernation clustering and its consequences for associative nest foundation in *Polistes dominulus* (Hymenoptera Vespidae). Behav Ecol Sociobiol 56:315–321

Dapporto L, Sledge MF, Turillazzi S (2005) Dynamics of cuticular chemical profiles of *Polistes dominulus* workers in orphaned nests. J Insect Physiol 51:969–973

Dapporto L, Santini A, Dani FR, Turillazzi S (2007) Workers of a *Polistes* paper wasp detect the presence of their queen by chemical cues. Chem Senses 32(8):795–802

Dawkins R (1976) The selfish gene. Oxford University Press, NewYork

Downs SG, Ratnieks FLW (2000) Adaptive shifts in honey bee (*Apis mellifera* L.) guarding behavior support predictions of the acceptance threshold model. Behav Ecol 9:326–333

Dettner K, Liepert C (1994) Chemical mimicry and camouflage. Ann Rev Entomol 39(1):129–154

d'Ettorre P, Errard C (1999) Trophallaxie proctodéale chez la fourmi esclavagiste *Polyergus rufescens*. Actes Coll Insectes Soc 12:61–64

d'Ettorre P, Heinze J (2005) Individual recognition in ant queens. Curr Biol 15:2170–2174

d'Ettorre P, Lenoir A (2010) Nestmate recognition. In: Lach L, Parr CL, Abbott KL (eds) Ant ecology. Oxford University Press, Oxford, pp 194–209

d'Ettorre P, Mondy N, Lenoir A, Errard C (2002) Blending in with the crowd: social parasites integrate into their host colonies using a flexible chemical signature. Proc R Soc Lond B 269:1911–1918

d'Ettorre P, Wenseleers T, Dawson J, Hutchinson S, Boswell T, Ratnieks FLW (2006) Wax combs mediate nestmate recognition by guard honey bees. Anim Behav 71:773–779

Dreier S, d'Ettorre P (2009) Social context predicts recognition systems in ant queens. J Evol Biol 22(3):644–649

Dreier S, van Zweden JS, d'Ettorre P (2007) Long term memory of individual identity in ant queens. Biol Lett 17:459–462

Erber J, Masuhr TH, Menzel R (1980) Localization of short-term memory in the brain of the bee, *Apis mellifera*. Behav Neural Biol 62:259–263

Errard C (1994a) Development of interspecific recognition behavior in the ants *Manica rubida* and *Formica selysi* (Hymenoptera: Formicidae) reared in mixed-species groups. J Insect Behav 7:83–99

Errard C (1994b) Long-term memory involved in nestmate recognition in ants. Anim Behav 48:263–271

Errard C, Fresneau D, Heinze J, Francoeur A, Lenoir A (1997) Social organization in the guest-ant *Formicoxenus provancheri*. Ethology 103:149–159

Errard C, Hefetz A, Jaisson P (2006) Social discrimination tuning in ants: template formation and chemical similarity. Behav Ecol Sociobiol 59(3):353–363

Espelie KE, Hermann HR (1990) Surface lipid of the social wasp *Polistes annularis* (L.) and its nest and nest pedicel. J Chem Ecol 16:1841–1852

Espelie KE, Wenzel JW, Chang G (1990) Surface lipids of social wasp *Polistes metricus* say and its nest and pedicel and their relation to nestmate recognition. J Chem Ecol 16:2229–2241

Fahrbach SE, Strande JL, Robinson GE (1995) Neurogenesis is absent in the brains of adult honey bees and does not explain behavioural neuroplasticity. Neurosci Lett 197:145–148

Farris SM, Robinson GE, Davis RL, Fahrbach SE (1999) Larval and pupal development of the mushroom bodies in the honey bee. Apis mellifera J Comp Neurol 414:97–113

Fénéron R, Jaisson P (1995) Ontogeny of nestmate brood recognition in a primitive ant, *Ectatomma tubercalutum* Olivier (Ponerinae). Anim Behav 50(1):9–14

Foitzik S, DeHeer CJ, Hunjan DN, Herbers JM (2001) Coevolution in host-parasite systems: behavioural strategies of slave-making ants and their hosts. Proc R Soc Lond B 268:1139–1146

Foubert E, Nowbahari E (2008) Memory span for heterospecific individuals'odors in an ant, *Cataglyphis cursor*. Learn Behav 36:319–326

Gamboa GJ (1988) Sister, aunt-niece, and cousin recognition by social wasps. Behav Genet 18:409–423

Gamboa GJ (2004) Kin recognition in eusocial wasps. Ann Zool Fennici 41:789–808

Gamboa GJ, Reeve HK, Pfennig DW (1986a) The evolution and ontogeny of nestmate recognition in social wasps. A Rev Entomol 31:431–454

Gamboa GJ, Reeve HK, Ferguson I, Wacker TL (1986b) Nestmate recognition in social wasps: the origin and acquisition of recognition odours. Anim Behav 34:685–695

Getz WM, Smith KB (1983) Genetic kin recognition: honey bees discriminate between full and half sisters. Nature 302:147–148

Getz WM, Smith KB (1986) Honey bee kin recognition: learning self and nestmate phenotypes. Anim Behav 34:1617–1626

Greene MJ, Gordon DM (2003) Social insects cuticular hydrocarbons inform task decisions. Nature 423:32

Gronenberg W, Heeren S, Hölldobler B (1996) Age-dependent and task-related morphological changes in the brain and the mushroom bodies of the ant *Camponotus floridanus*. J Exp Biol 199:2011–2019

Guerrieri FJ, Nehring V, Jørgensen CG, Nielsen J, Galizia CG, d'Ettorre P (2009) Ants recognize foes and not friends. Proc R Soc B 276:2461–2468

Guerrieri FJ, d'Ettorre P, Devaud JM, Giurfa M (2011) Long- term olfactory memories are stabilised via protein synthesis in *Camponotus fellah* ants. J Exp Biol 214:3300–3304

Hadley NF (1994) Water relations of terrestrial arthropods. Academic Press, San Diego

Hamilton WD (1964) The genetical evolution of social behaviour. J Theor Biol 7:1–50

Hamilton WD (1987) Discrimination nepotism: expectable, common, overlooked. In: Fletcher DJC, Michener CD (eds) Kin recognition in animals. Wiley, New York, pp 417–437

Harano K, Sasaki M (2006) Renewal process of nestmate recognition template in European honeybee *Apis mellifera* L. (Hymenoptera: Apidae). Appl Entomol Zool 41(2): 325–330

Hare JF, Alloway TM (2001) Prudent *Protomognathus* and despotic *Leptothorax duloticus*: differential costs of ant slavery. Proc Natl Acad Sci USA 98:12093–12096

Hefetz A (2007) The evolution of hydrocarbon pheromone parsimony in ants (Hymenoptera: Formicidae)—interplay of colony odor uniformity and odor idiosyncrasy: a review. Myrmecol News 10:59–68

Heimbeck G, Bugnon V, Gendre N, Häberlin C, Stocker RF (1999) Smell and taste perception in *D. melanogaster* larva: toxin expression studies in chemosensory neurons. J Neurosci 19:6599–6609

Heisenberg M (1994) Central brain function in insects: genetic studies on the mushroom bodies and central complex in *Drosophila*. Forts Zool 39:30–39

Heisenberg M (1998) What do the mushroom bodies do for the insect brain? Intro Learn Mem 5(1):1–10

Hepper PG (1987) The amniotic fluid: an important priming role in kin recognition. Anim Behav 35(5):1343–1346

Hepper PG, Waldman B (1992) Embryonic olfactory learning in frogs. Q J Exp Psychol B 44(3–4): 179–197

Hepper PG (2003) Prenatal psychological and behavioural development. In: Valsiner J, Connolly KJ (eds) The handbook of developmental psychology. Sage, London, pp 91–114

Hölldobler B, Michener CD (1980) Mechanisms of identification and discrimination in social Hymenoptera. In: Markl H (ed) Evolution of social behavior: hypotheses and empirical tests. VC, Weinheim, pp 35–58

Hölldobler B, Wilson EO (1990) The ants. Belknap Press, Cambridge, p 732

Holman L, Jørgensen CG, Nielsen J, d'Ettorre P (2010) Identification of an ant queen pheromone regulating worker sterility. Proc R Soc B 277(1701):3793–3800

Holman L, Leroy C, Jørgensen C, Nielsen J, d'Ettorre P (2013) Are queen ants inhibited by their own pheromone? Regulation of productivity via negative feedback. Behav Ecol 24(2):380–385

Holmes WG, Sherman PW (1982) The ontogeny of kin recognition in two species of ground squirrels. Am Zool 22:491–517

Hudson R (1993) Olfactory imprinting. Current Opin Neurobiol 3(4):548–552

Ichinose K, Lenoir A (2010) Hydrocarbons detection levels in ants. Insect Soc 57:453–455

Isingrini M, Lenoir A, Jaisson P (1985) Preimaginal learning as a basis of colony brood recognition in the ant *Cataglyphis cursor*. Proc Nat Acad Sci, USA 82:8545–8547

Ito K, Hotta Y (1992) Proliferation pattern of postembryonic neuroblasts in the brain of *Drosophila melanogaster*. Dev Biol 149:134–148

Jaisson P (1972) Mise en évidence d'une phéromone d'attractivité produite la jeune ouvrière *Formica* (Hymenoptera : Formicidae). C R Acad Sci Paris Ser D 274:429–432

Jaisson P (1980) Environmental preference induced experimentally in ants (Hymenoptera: Formicidae). Nature 286:388–389

Jaisson P (1987) The construction of fellowship between nestmates in social hymenoptera. In: Pasteels JM, Deneubourg JL (eds) Experientia supplementum 54. From individual to collective behaviour in social insects. Birkhauser Verlag, Basel, pp 313–331

Jaisson P (1991) Kinship and fellowship in ants and social wasps. In. Hepper PG (ed) Kin recognition. Cambridge University Press, Cambridge, pp 60–93

Jeanson R, Weidenmüller A (2013) Interindividual variability in social insects–proximate causes and ultimate consequences. Biol Rev, pp 671–687

Johnson CA, Vander Meer RK, Lavine B (2001) Changes in the cuticular hydrocarbon profile of the slave-maker ant queen, *Polyergus breviceps* Emery, after killing a *Formica* host queen (Hymenoptera: Formicidae). J Chem Ecol 27(9):1787–1804

Johnson BR, van Wilgenburg E, Tsutsui ND (2011) Nestmate recognition in social insects: overcoming physiological constraints with collective decision making. Behav Ecol Sociobiol 65(5):935–944

Jutsum AR, Saunders TS, Cherrett JM (1979) Intraspecific aggression in the leaf-cutting ant *Acromyrmex octospinosus*. Anim Behav 27:839–844

Kaib M, Heinze J, Ortius D (1993) Cuticular hydrocarbons profiles in the slave-making ant *Harpogoxenus sublaevis* and its hosts. Naturwissenschaften 80:281–285

Keegans SJ, Morgan ED, Turillazzi S, Jackson BD, Billen J (1993) The dufour gland and the secretion placed on eggs of two species of social wasps, *Liostenogaster flavolineata* and *Parischnogaster jacobsoni* (Vespidae: Stenogastrinae). J Chem Ecol 19:279–290

Lahav S, Soroker V, VanderMeer RK, Hefetz A (2001) Segregation of colony odor in the desert ant *Cataglyphis niger*. J Chem Ecol 27:927–943

Lambardi D, Dani FR, Turillazzi S, Boomsma JJ (2007) Chemical mimicry in an incipient leaf-cutting ant social parasite. Behav Ecol Sociobiol 61(6):843–851

Lee T, Lee A, Luo L (1999) Development of the *Drosophila* mushroom bodies: sequential generation of three distinct types of neurons from a neuroblast. Development 126:4065–4076

Lenoir A, Errard C, Francoeur A, Loiselle R (1992) Relations entre la fourmi parasite *Formicoxenus provancheri* et sur hôte *Myrmica incompleta*. Données biologiques et éthologiques (Hym. Formicidae). Insect Soc 39:81–97

Lenoir A, Fresneau D, Errard C, Hefetz A (1999) Individuality and colonial identity in ants: the emergence of the social representation concept. In: Detrain C, Deneubourg J-L, Pasteels JM (eds) Information processing in social insects. Birkhäuser Verlag, Basel, pp 219–237

Lenoir A, d'Ettorre P, Errard C, Hefetz A (2001) Chemical ecology and social parasitism in ants. Annu Rev Entomol 46:573–599

Lenoir A, Depickere S, Devers S, Christides JP, Detrain C (2009) Hydrocarbons in the ant *Lasius niger*: from the cuticle to the nest and home range marking. J Chem Ecol 35:913–921

Leonhardt SD, Brandstaetter AS, Kleineidam CJ (2007) Reformation process of the neuronal template for nestmate-recognition cues in the carpenter ant *Camponotus floridanus*. J Comp Physiol 193:993–1000

Liebig J (2010) Hydrocarbon profiles indicate fertility and dominance status in ant, bee, and wasp colonies. Insect hydrocarbons: biology, biochemistry, and chemical ecology. Cambridge University Press, Cambridge, pp 254–281

Liebig J, Peeters C, Oldham NJ, Markstädter C, Hölldobler B (2000) Are variations in cuticular hydrocarbons of queens and workers a reliable signal of fertility in the ant *Harpegnathos saltator*? Proc Natl Acad Sci USA 97:4124–4131

Liu Z, Yamane S, Wang Q, Yamamoto H (1998) Nestmate recognition and temporal modulation in the patterns of cuticular hydrocarbons in natural colonies of Japanese carpenter ant *Camponotus japonicus* Mayr (Hymenoptera: Formicidae). J Ethol 16:57–65

Lockey KH (1988) Lipids of the insect cuticle: origin composition and function. Comp Biochem Physiol 89B:595–645

Lorenzi MC (1992) Epicuticular hydrocarbons of *Polistes biglumis bimaculatus* (Hymenoptera, Vespidae): preliminary results. Ethol Ecol Evol 3: 61–63, (Special Issue)

Lorenzi MC, Bagnères AG (1996) Hydrocarbon pattern variations in the paper of *Polistes biglumis bimaculatus* nests usurped or not by the social parasite *Polistes atrimandibularis* (Hymenoptera Vespidae). Proc XX Int Congr Entomol Firenze 416:13–107

Lorenzi MC, Bagnères AG, Clément JL (1996) The role of cuticular hydrocarbons in insect societies: is it the same in paper wasps? In: Turillazzi S, West Eberhard MJ (eds) Natural history and the evolution of paper wasps. Oxford University Press, Oxford, pp 178–189

Lorenzi MC, Cometto I, Marchisio G (1999) Species and colony components in the recognition odor of young social wasps: their expression and learning (*Polistes biglumis* and *P. atrimandibularis*; Hymenoptera: Vespidae). J Insect Behav 12(2):147–158

Lorenzi MC, Sledge MF, Laiolo P, Sturlini E, Turillazzi S (2004) Cuticular hydrocarbon dynamics in young adult *Polistes dominulus* (Hymenoptera: Vespidae) and the role of linear hydrocarbons in nestmate recognition systems. J Insect Physiol 50:935–941

Lorenzi MC, Caldi M, Cervo R (2007) The chemical strategies used by *Polistes nimphus* social wasp usurpers (Hymenoptera Vespidae). Biol J Linn Soc 91:505–512

Lorenzi MC, Cervo R, Bagneres A-G (2011) Facultative social parasite mark host nests with branched hydrocarbons. Anim Behav 42(5):1143–1149

Martin SJ, Vitikainen E, Helanterä H, Drijfhout FP (2008) Chemical basis of nest-mate discrimination in the ant *Formica exsecta*. Proc R Soc B 275(1640):1271–1278

Masson C, Pham-Delègue MH, Fonta C, Gascuel J, Arnold G, Nicolas G, Kerszberg M (1993) Recent advances in the concepts of adaptation to natural odour signals in the honeybee, *Apis mellifera* L. Apidologie 24:169–194

Mateo JM (2004) Recognition systems and biological organization: the perception component of recognition. Ann Zool Fennici 41:729–745

Menzel R (1993) Associative learning in honey bees. Apidologie 24:157–168

Meskali M, Bonavita-Cougourdan A, Provost E, Bagnères AG, Dusticier G, Clément JL (1995) Mechanism underlying cuticular hydrocarbon homogeneity in the ant *Camponotus vagus* (SCOP.)(Hymenoptera: Formicidae): role of postpharyngeal glands. J Chem Ecol 21(8):1127–1148

Michener CD, Smith BH (1987) Kin recognition in primitively social insects. In: Fletcher DJC, Michener CD (eds) Kin recognition in animals. John Wiley and Sons Press, Chichester, pp 209–242

Mintzer A, Vinson SB (1985) Kinship and incompatibility between colonies of the acacia-ant *Pseudomyrmex ferruginea*. Behav Ecol Sociobiol 17:75–78

Mitra A, Ramachandran A, Gadagkar R (2014) Nestmate discrimination in the social wasp *Ropalidia marginata*: chemical cues and chemosensory mechanism. Anim Behav 88:113–124

Monnin T (2006) Chemical recognition of reproductive status in social insects. Ann Zool Fenn 43:515–530

Morel L (1983) Relation entre comportement agressif et privation sociale précoce chez les jeunes fourmis immatures de la fourmi *Camponotus vagus* Scop. (Hymenoptera: Formicidae). C R Hebd Séances. Acad Sci Série D 296:449–452

Morel L (1988) Ontogènese de la reconnaissance des membres de la société chez *Camponotus floridanus* (Hymenoptera: Formicidae). Role de l'expérience sociale précoce. Biologie du Comportement 13:59–72

Newey PS, Robson SKA, Crozier RH (2009) Temporal variation in recognition cues: implications for the social life of weaver ants *Oecophylla smaragdina*. Anim Behav 77:481–488

Nielsen J, Boomsma JJ, Oldham NJ, Petersen HC, Morgan ED (1999) Colony level and season-specific variation in cuticular hydrocarbon profiles of individual workers in the ant *Formica truncorum*. Insect Soc 46:58–65

Nowbahari E, Lenoir A (1989) Age related changes in aggression in ant *Cataglyphis cursor* (Hymenoptera, Formicidae). Behav Process 18:173–181

Ozaki M, Hefetz A (2014) Neural mechanisms and information processing in recognition systems. Insects 5:722–741

Ozaki M, Wada-Katsumata A (2010) Perception and olfaction of cuticular compounds. In: Blomquist GJ, Bagnères AG (eds) Insect hydrocarbons: biology, biochemistry and chemical ecology. Cambridge University Press, Cambridge, pp 207–221

Ozaki M, Wada-Katsumata A, Fujikawa K, Iwasaki M, Yokohari F, Satoji Y, Nisimura T, Yamaoka R (2005) Ant nestmate and non-nestmate discrimination by a chemosensory sensillum. Science 309:311–314

Page RE, Breed ME (1987) Kin recognition in social bees. Trends Ecol Evol 2:272–275

Panek LM, Gamboa GJ, Espelie KE (2001) The effect of a wasp's age on its cuticular hydrocarbon profile and its tolerance by nestmate and non-nestmate conspecifics (*Polistes fuscatus*, Hymenoptera: Vespidae). Ethology 107:55–63

Pauls D, Selcho M, Gendre N, Stocker RF, Thum AS (2010) *Drosophila* larvae establish appetitive olfactory memories via mushroom body neurons of embryonic origin. J Neurosci 30:10655–10666

Peeters C, Monnin T, Malosse C (1999) Cuticular hydrocarbons correlated with reproductive status in a queenless ant. Proc R Soc Lond B 266:1323–1327

Pfenning DW, Reeve HK, Shellmann JS (1983a) Learned component of nestmate discrimination in workers of a social wasp, *Polistes fuscatus* (Hymenoptera, Vespidae). Anim Behav 31:412–416

Pfenning DW, Gamboa GJ, Reeve HK, Shellmann JS, Reeve JS, Ferguson ID (1983b) The mechanism of nestmate discrimination in social wasps (Hymenoptera: Vespidae). Behav Ecol Sociobiol 13:299–305

Provost E, Blight O, Tirard A, Renucci M (2008) Hydrocarbons and insects' social physiology. In: Maes RP (ed) Insect physiology: new research. Nova Science Publishers, New York, pp 19–72

Python F, Stocker RF (2002) Adult-like complexity of the larval antennal lobe of *D. melanogaster* despite markedly low numbers of odorant receptor neurons. J Comp Neurol 445:374–387

Ramaekers A, Magnenat E, Marin EC, Gendre N, Jefferis GSXE, Luo L, Stocker RF (2005) Glomerular maps without cellular redundancy at successive levels of the *Drosophila* larval olfactory circuit. Curr Biol 15:982–992

Ratnieks FL (1991) The evolution of genetic odor-cue diversity in social Hymenoptera. Am Nat pp 202–226

Ray S (1999) Survival of olfactory memory through metamorphosis in the fly *Musca domestica*. Neurosci Lett 259:37–40

Reeve HK (1989) The evolution of conspecific acceptance thresholds. Am Nat 133:407–435

Robinson SR, Smotherman WP (1991) Fetal learning: implications for the development of kin recognition. In: Hepper PG (ed) kin recognition. Cambridge University Press, Cambridge, England, pp 308–334

Ross NM, Gamboa GJ (1981) Nestmate discrimination in social wasps (*Polistes metricus*, Hymenoptera: Vespidae). Behav Ecol Sociobiol 9:163–165

Schaal B, Marlier L, Soussignan R (2000) Human fetuses learn odours from their pregnant mother's diet. Chem Sens 25:729–737

Shellman JS, Gamboa GJ (1982) Nestmate discrimination in social wasps: the role of exposure to nest and nestmates. Behav Ecol Sociobiol 11:51–53

Signorotti L, Cappa F, d'Ettorre P, Cervo R (2014a) Novel insights into the ontogeny of nestmate recognition in *Polistes* social wasps. PLoS ONE 9(5):e97024

Signorotti L, Jaisson P, d'Ettorre P (2014b) Larval memory affects adult nestmate recognition in the ant *Aphaenogaster senilis*. Proc R Soc B 281:20132579

Singer TL (1998) Roles of hydrocarbons in the recognition systems of insects. Am Zool 38(2):394–405

Singer TL, Espelie KE (1992) Social wasps use nest paper hydrocarbons for nestmate recognition. Anim Behav 44(1):63–68

Singer TL, Camann MA, Espelie KE (1992) Discriminant analysis of cuticular hydrocarbons of social wasp *Polistes exclamans* Viereck and surface hydrocarbons of its nest paper and pedicel. J Chem Ecol 18:785–797

Singh RN, Singh K (1984) Fine structure of the sensory organs of *Drosophila melanogaster* Meigen larva (Diptera: Drosophilidae). Int J Insect Morphol Embryol 13:255–273

Sledge MF, Trinca I, Massolo A, Boscaro F, Turillazzi S (2004) Variation in cuticular hydrocarbon signatures, hormonal correlates and establishment of reproductive dominance in a polistine wasp. J Insect Physiol 50:73–83

Soroker V, Vienne C, Hefetz A, Nowbahari E (1994) The postpharyngeal gland as a “gestalt” organ for nestmate recognition in the ant *Cataglyphis niger*. Naturwissenschaften 81:510–513

Soroker V, Vienne C, Hefetz A (1995) Hydrocarbon dynamics within and between nestmates in *Cataglyphis niger* (Hymenoptera: Formicidae). J Chem Ecol 21(3):365–378

Soroker V, Fresneau D, Hefetz A (1998) Formation of colony odor in ponerine ant *Pachycondyla apicalis*. J Chem Ecol 24(6):1077–1090

Soroker V, Lucas C, Simon T, Fresneau D, Durand JL, Hefetz A (2003) Hydrocarbon distribution and colony odour homogenization in *Pachycondyla Apicalis*. Insect Soc 50:212–217

Starks PT (2004) Recognition systems: from components to conservation. In: Annales Zoologici Fennici, vol 41(6). Suomen Biologian Seura Vanamo, Helsinki, pp 689–690 (1964-)

Stroeymeyt N, Guerrieri FJ, van Zweden JS, d’Ettorre P (2010) Rapid decision-making with side-specific perceptual discrimination in ants. PLoS ONE 5(8):e12377

Stuart RJ (1987a) Nestmate recognition in leptothoracine ants: testing Fielde’s progressive odor hypothesis. Ethology 76(2):116–123

Stuart RJ (1987b) Individual workers produce colony-specific nestmate recognition cues in the ant, *Leptothorax curvispinosus*. Anim Behav 35:1062–1069

Stuart RJ (1988) Collective cues as a basis for nestmate recognition in polygynous leptothoracine ants. Proc R Soc B 85(12):4572–4575

Stuart RJ (1992) Nestmate recognition and the ontogeny of acceptability in the ant, *Leptothorax curvispinosus*. Behav Ecol Sociobiol 30:403–408

Sturgis S, Gordon DM (2012) Nestmate recognition in ants (Hymenoptera, Formicidae): a review. Myrmecological News 16:101–110

Tibbetts EA (2002) Visual signals of individual identity in the wasp *Polistes fuscatus*. Proc R Soc B 269(1469):1423–1428

Tissot M, Stocker RF (2000) Metamorphosis in *Drosophila* and other insects: the fate of neurons throughout the stages. Prog Neurobiol 62(1):89–111

Turillazzi S (1985) Function and characteristics of the abdominal substance secreted by wasps of the genus *Parischnogaster* (Hymenoptera Stenogastrinae). Monit Zool Ital 19:91–99

Turillazzi S, Cervo R, Cavallari I (1990) Invasion of the nest of *Polistes dominulus* by the social parasite *Sulcopolistes sulcifer* (Hymenoptera, Vespidae). Ethology 84:47–59

Turillazzi S, Sledge MF, Dani FR, Cervo R, Massolo A, Fondelli L (2000) Social hackers: integration in the host chemical recognition system by a paper wasp social parasite. Naturwissenschaften 87(4):172–176

Turillazzi S, Fanelli D, Theodora P, Lambardi D, Ortolani I, Hashim R, Baracchi D (2008) Determinants of immature brood and nest recognition in a stenogastrine wasp (Hymenoptera Vespidae). Ethol Ecol Evol 20(1):17–33

Tully T, Cambiazo V, Kruse L (1994) Memory through metamorphosis in normal and mutant *Drosophila*. J Neurosci 14:68–74

Vander Meer RK, Morel L (1998) Nestmate recognition in ants. In: Vander Meer RK, Breed MD, Winston M, Espelie C (eds) Pheromone communication in social insects: ants, wasps, bees and termites, pp 79–103

Van Hooser CA, Gamboa GJ, Fishwild TG (2002) The function of abdominal stroking in the paper wasp, *Polistes fuscatus* (Hymenoptera Vespidae). Ethol Ecol Evol 14(2):141–148

Van Oystaeyen A, Oliveira RC, Holman L, van Zweden JS, Romero C, Oi CA, d'Ettorre P, Khalesi M, Billen J, Wäckers F, Millar JG, Wenseleers T (2014) Conserved class of queen pheromones stops social insect workers from reproducing. Science 343(6168):287–290

van Zweden JS, d'Ettorre P (2010) Nestmate recognition in social insects and the role of hydrocarbons. In: Blomquist GJ, Bagnères AG (eds) Insect hydrocarbons: biology, biochemistry and chemical ecology. Cambridge University Press, Cambridge, pp 222–243

van Zweden JS, Dreier S, d'Ettorre P (2009) Disentangling environmental and heritable nestmate recognition cues in a carpenter ant. J Insect Physiol 55:158–163

van Zweden JS, Brask JB, Christensen JH, Boomsma JJ, Linksvayer TA, d'Ettorre P (2010) Blending of heritable recognition cues among ant nestmates creates distinct colony gestalt odours but prevents within-colony nepotism. J Evol Biol 23(7):1498–1508

Vienne C, Bagnères AG, Lange C, Errard C (1990) Etude chimique de la reconnaissance interindividuelle chez *Myrmica rubra* et *Manica rubida* (Formicidae, Myrmicinae) élevées en colonies mixtes artificielles. Actes Colloq Insectes Soc 6:261–265

Vienne NC, Soroker V, Hefetz A (1995) Congruency of hydrocarbon patterns in heterospecific groups of ants: transfer and/or biosynthesis? Insect Soc 42(3):267–277

Wagner D, Brown MJF, Broun P, Cuevas W, Moses LE, Chao DL, Gordon DM (1998) Task related differences in the cuticular hydrocarbon composition of harvester ants, *Pogonomyrmex barbatus*. J Chem Ecol 24:2021–2037

Waldman B (1988) The ecology of kin recognition. Ann Rev Ecol Syst 19:543–571

Wilson EO (1971) The insect societies. Belknap Press of Harvard University Press, Cambridge

Zacchi F, Cervo R, Turillazzi S (1996) How *Polistes semenowi*, obligate social parasite, invades the nest of its host, *Polistes dominulus* (Hymenoptera, Vespidae). Insect Soc Life 1:125–130

Zahavi A (1977) Reliability in communication system and the evolution of altruism. In: Stonehous B, Perrins C (eds) Evolutionary ecology. University Park Press, Baltimore

Chapter 11
Communication and Social Regulation in Termites

Anne-Geneviève Bagnères and Robert Hanus

Abstract Communication and social regulation are among the distinguishing features of termites: they are part of all basic aspects of termite biology, from ontogeny and caste differentiation to social behavior and cooperation. As in other highly social taxa, communication in termites predominantly relies on a complex network of chemical signals, which are complemented by vibration-based signals. In contrast to other social taxa, the role of visual cues is negligible. In this chapter, we review the recent literature on the different components that make up termite communication and social regulation systems by tracing termite evolution and examining the role played by different factors, such as sex and caste, and different behaviors, such as those related to defense, nestmate recognition, egg and brood care, foraging, and nest building, among others. The main characteristics of termites are compared to those of other social insects in the introduction. In the first section, we review the most important researches on termite communication and social regulation that are related to social activities in the basal phylogenetic lineages, and in the Termitidae (higher termites), the most advanced and diversified family. The abundant literature on the best studied genera, *Reticulitermes*, *Coptotermes*, and *Heterotermes*, which are considered for the purposes of this chapter to be intermediate termites, is reviewed and discussed separately in the second section. By using this approach, we seek to describe communication and social regulation systems in basal and primitive termites and illustrate how they have evolved to become more complex in intermediate and higher termites.

A.-G. Bagnères (✉)
Institut de Recherche sur la Biologie de l’Insecte, UMR CNRS 7261,
Université F. Rabelais, UFR Sciences et Techniques, Parc Grandmont, 37200 Tours, France
e-mail: bagneres@univ-tours.fr

R. Hanus
Chemistry of Social Insects, Institute of Organic Chemistry and Biochemistry,
Academy of Sciences of the Czech Republic, Flemingovo nám. 2, 16610 Prague,
Czech Republic
e-mail: robert@uochb.cas.cz

L. Aquiloni and E. Tricarico (eds.), *Social Recognition in Invertebrates*,
DOI 10.1007/978-3-319-17599-7_11

Introduction

Termites are classified in the order Isoptera, which contains nearly 3000 species organized into 282 genera (Krishna et al. 2013). Traditionally, seven families are recognized, ranging from the most basal to the most advanced (Mastotermitidae, Termopsidae, Hodotermitidae, Kalotermitidae, Serritermitidae, Rhinotermitidae, and Termitidae) (e.g., Cancello and DeSouza 2004; Inward et al. 2007a), although some new phylogenetic scenarios split the basal lineages into more families (e.g., Engel et al. 2009). Termites evolved from non- or subsocial wood-feeding cockroaches, and the sister taxon for the group is the cockroach genus *Cryptocercus*. Some authors have even described termites as social cockroaches (Inward et al. 2007b) and have recently placed them in the order Blattodea in the superorder Dictyoptera, making them the only eusocial members of these taxa (Pellens et al. 2007). Here, however, we will use the more conventional classification scheme, considering Isoptera as an order containing the seven traditional families (Misof et al. 2014). The Rhinotermitidae occupy a key position on the evolutionary pathway of Isoptera: they mark the separation between lower and higher termites. This family contains socially primitive termites, such as the genera *Prorhinotermes* and *Termitogeton*, as well as more socially advanced genera, such as *Coptotermes* and *Reticulitermes*. The most advanced termites form a monophyletic family, the Termitidae, which is ecologically dominant in terms of abundance and species richness; over 70 % of all living termite species belong to this group (Krishna et al. 2013). Termites are of crucial ecological significance since they decompose plant material, such as wood, grass, and leaf litter, and modify the distribution and properties of soils (Bignell and Eggleton 2000). Even though termites are, by far, the most abundant in the tropics, their distribution in nature is actually very broad, ranging from the northern Palearctic to the temperate rainforests of New Zealand. African rainforests contain the greatest number of genera, whereas temperate rainforests are generally species poor; termites also occur in semi-desert and savanna woodland ecosystems (Jones and Eggleton 2011). Their distribution range greatly expands when we take into account urban habitats and introduced ranges, but cities such as Toronto or Hamburg seem to represent their northern limits. In this introduction, we review the primary reasons why communication and social regulation are so important in the different termite families.

Studies on termite social evolution and phylogeny mainly focus on the evolution of the worker caste, but they also examine differences in nest building and foraging patterns as well as the presence or absence of symbionts and their coevolution with termite hosts (Eggleton 2011; Lo and Eggleton 2011). While the evolutionary origin of true workers (i.e., workers that remain workers and cannot further develop into other castes; also see below) is still a topic of debate, it is nonetheless helpful to separate termite lineages and genera according to the complexity of their life histories (Lo et al. 2009) since the occurrence of true workers is linked with complex nesting patterns and foraging for food outside the nest (Legendre et al. 2008, 2013). The presence of a true worker caste is a key feature when it comes to classifying termites, with a few exceptions in the case of the Mastotermitidae and Hodotermitidae; it is assumed that this feature is a synapomorphy shared by the more advanced Rhinotermitidae and all the Termitidae (Legendre et al. 2013). Thus, termites without a true worker caste are called "one-piece-type" termites: they form small colonies and inhabit a single piece of wood upon which they also feed. This type of social organization, which is found in the Kalotermitidae, Termopsidae, and some Rhinotermitidae (*Prorhinotermes*, *Termitogeton*), as well as the Serritermitidae (*Glossotermes*), is generally considered to be primitive (Roisin and Korb 2011). More advanced social organization is observed in "separate-type" termites: they are characterized by a true worker caste, forage for food outside the nest (which they often build de novo), and usually live in large colonies, which can reach up to a few million individuals in extreme cases (Abe 1987, 1990; Shellman-Reeve 1997). In termite evolution, the transition from one-piece-type nesting to separate-type nesting was accompanied by an increase in the complexity of social interactions and communication as well as by the development of different modes of signaling; for instance, there was a switch from short-range to long-range signals. Since this major transition in termite biology has occurred several times in various lineages over the course of termite social evolution (Legendre et al. 2008), it is not easy to address all these specific cases in a comprehensive way. Therefore, for simplicity's sake, we have structured this chapter as mentioned above. First, we describe and contrast social recognition in basal versus more advanced termites. Second, we focus in greater detail on the best studied genera in the family Rhinotermitidae, namely *Coptotermes*, *Reticulitermes*, and *Heterotermes*, which are intermediate termites.

During the complex *evolution of sociality*, some insect taxa have not become eusocial because the different types of intragroup cooperation (parent/offspring, brood care, etc.) in which they engage do not involve overlapping generations, and more importantly, no reproductive division of labor is present (Costa 2006). In their comparison of the social biology of basal ants and termites, Thorne and Traniello (2002) explain that disease resistance and management, which influence the reproductive organization of colonies and their division of labor (which are also strongly influenced by nesting and feeding ecology), may have been significant factors in the evolution of sociality since social insects are particularly vulnerable to infections (Wilson-Rich et al. 2009). Self-medication is widespread in animals (de Roode et al. 2013), but social insects develop a plethora of other strategies to resist pathogens, including associations with symbiotic organisms (Chouvenc et al. 2013; de Souza et al. 2013). Corpse management is another essential adaptation to social life (Sun and Zhou 2013). The soldiers of many termite species produce potent defensive secretions that can have antifungal and antibacterial properties (Rosengaus et al. 2000; Zhao et al. 2004; Fuller 2007). Furthermore, in some species, workers that have been inoculated with an entomopathogenic fungus may respond by rapidly initiating cellular encapsulation; this individual immune reaction can save the entire colony (Chouvenc et al. 2009). The benefits of a better defense against pathogens may have driven certain aspects of social life, such as allogrooming, brood care, and intracolonial communication (Roisin and Korb 2011; Korb et al. 2012). Greater group size not only increases a group's ability to defend against all kinds of predators, but it also protects that group against disease (Gao et al. 2012). In termite species that have large colonies, more and more sophisticated solutions must have been evolving in terms of the division of labor between and within castes. Defense against macro-predators such as ants may have also played a key role in shaping termite caste evolution; for instance, more vigorous dealate males seem to be under selective pressure to become better fighters (Li et al. 2013). Altruistic behavior thus provides a further layer of colony protection. The chemical, mechanical, and behavioral adaptations of soldiers, which are permanently sterile defenders, appear to have been shaped above all by the predation pressure exerted by ants.

The development of termite castes is of particular interest when studying the evolution of sociality because, in comparison to other eusocial insects, termites demonstrate a high degree of polymorphism as well as a significant amount of polyphenism as a result of their hemimetabolous development. Both males and females are present in all societies, although the sex ratio may vary depending on the caste (Muller and Korb 2008; Roisin and Korb 2011). Hemimetabolous development in termites allows for a significant degree of plasticity: an undifferentiated larva can become either a worker or a nymph and more advanced larval stages (workers and nymphs) can eventually develop into soldiers, neotenics (brachypterous neotenics that develop from nymphs and apterous neotenics that develop from workers), or adults (alate imagoes, i.e., primary reproductives). This temporal developmental polymorphism appears to be unique among insects (Noirot 1989). Termites also exhibit a high degree of neoteny (the ability of immature forms to reproduce); workers and nymphs can rapidly initiate individual reproduction without leaving the natal nest and without becoming adults. This trait is essential to their remarkable reproductive flexibility (Myles 1999) and has led to a wide variety of social structures (Shellman-Reeve 1997), from the one-piece-type termites, whose immatures retain the ability to reproduce at all stages, to the advanced separate-type species, whose workers are almost all permanently sterile. Nevertheless, in one-piece-type termites, for whom wood serves as both food and shelter, workers take less risks and have more developmental plasticity; however, the probability that a given reproductive couple will successfully found a new nest is very low, because of the risky dispersal option, as it has been shown for *Cryptotermes secundus* with less than 1 % success of new foundings. In contrast, in multiple-site nesters, who take more risks foraging outside, the different castes have irreversible development but more individuals are available for nest defense and there is a greater probability that a given colony will persist (Roisin and Korb 2011). It is therefore more common to find completely sterile workers among hymenopterans than termites (Howard and Thorne 2011). The extremely altruistic defense behavior displayed by some termite castes is remarkable. For instance, soldiers of some species sacrifice themselves for the colony by causing their dehiscent defense glands to explode, a specialized suicidal adaptation (Bordereau et al. 1997); in other species, aged termites carry out suicide missions on behalf of their nestmates (Šobotník et al. 2010, 2012). Although the soldier caste in termites is relatively well defined, the worker caste, which has played a crucial role in the group's evolutionary success, is subject to much more debate with regards to its development, evolutionary origin, and function (Noirot 1982; Roisin and Korb 2011). In social insects, the processes underlying caste differentiation are often debated, but it is commonly thought that identifying the proximate mechanisms that lead to caste differentiation will yield a better understanding of termite phenotypic plasticity. Frequently, debate centers on the relative effects of genetics versus the environment (or ecology) on this type of polymorphism (Lo et al. 2009; Schwander et al. 2010; Simpson et al. 2011). Since the work of Prestwich et al. (1987), much has been discovered about the molecular, genomic, and integrative aspects of termite biology that has added to our understanding of termite caste differentiation (Brent 2009; Miura and Scharf 2011). In parallel, the processes involved in caste communication are much better characterized (see later in the chapter).

Social behavior and cooperation in termites have recently been thoroughly reviewed, in particular by Gardner and Foster as well as by Komdeur and colleagues in the Korb and Heinze book published in 2008. In social insects, the group benefits from the occurrence of large families. In termites, it would seem that the benefits of having numerous altruist individuals and enhanced reproductive efficiency have served to overcome the barriers to altruism linked with diplodiploidy. It is for this reason that the studies on certain termite species that show limited sociality, such as the wood-dwelling termites (*C. secundus*; Kalotermitidae), are of great interest. For instance, *C. secundus* has non-helping workers; its ecology also shows that when the termite nest is a bonanza-type food resource, there is no local resource competition between parents and their offspring or among siblings (Korb 2009). In this species, development is completely flexible and all workers are totipotent; this contrasts with what is seen in higher termites, which demonstrate much more rigid caste determination that yields true workers or terminally differentiated soldiers. In general, recognition processes allow individuals to determine whether their siblings will cooperate or compete with them. For example, in another kalotermid species, members of mature (i.e., alate-producing) colonies sabotage their siblings; they damage the wingpads of nymphs to prevent them from developing into new sexuals (Zimmermann 1983). One of the important recognition processes is trophallaxis, which is a behavior involved in sibling care. Brood care was a particularly important part of the phylogenetic switch from a wood-dwelling to a foraging lifestyle, a switch that occurred at the level of the Rhinotermitidae family. Interestingly, termites belonging to this latter family, such as the *Reticulitermes*, show more communication (Korb et al. 2012; Fig. 11.1).

Communication plays a central role in the recognition of nestmates or foreigners by social groups, which fits with the idea that communication is a key element in all social behavior. Indeed, Holldobler made the following comment in reference to EO Wilson's work (Costa 2006): "Study of communication mechanisms is at the core of any attempt to analyze social organization." Communication is particularly important for termites because they live in dark environments and most castes are blind. As a result, visual signaling does not appear to mediate

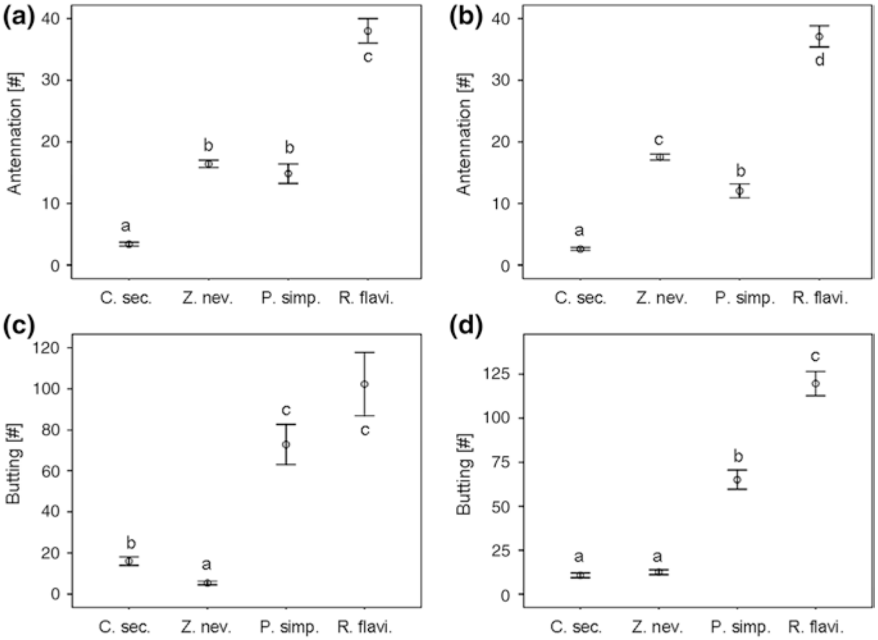


Fig. 11.1 Results of the comparison of interactive behaviors between species (Basal = *Cryptotermes secundus* (Termopsidae): C. sec., *Zootermopsis nevadensis* (Kalotermitidae): Z. nev., *Prorhinotermes simplex* (Rhinotermitidae): P. simp.; Intermediate = *Reticulitermes flavipes* (Rhinotermitidae): R. flavi.). Shown are mean values (±SE) of the frequency (#) during 30 min of focal observation for recipients of antennation. *Lower case letters* indicate significant differences between species ($P < 0.05$). From Korb et al. (2012) Brood care and social evolution in termites. Proc R Soc B, 279:2662–2671. http://rspb.royalsocietypublishing.org/content/suppl/2012/03/06/rspb.2011.2639.DC1.h

recognition in termites; instead, other means of communication are well developed. Communication mechanisms vary depending on nesting and foraging habits and are also affected by social organization. For instance, intracolonial vibroacoustic communication in social insects was reviewed in a publication by Hunt and Richard (2013). In termites, as in other social insects such as ants, wasps, or bees, social discrimination relies to a great degree on chemical cues, and cue diversity plays an important role in recognition (Breed and Buchwald 2009). Krasnec and Breed (2012) even compared social discrimination to self/non-self-recognition systems, such as the major histocompatibility complex. Adams (1991) was one of the first researchers to discover that nestmate recognition in termites is based on heritable odors. However, in general, reviewing literature on termites is lacking, which is reflected by the fact that, since the publication of Grassé's Termitologia in 1982, 1984 and 1986, only two books entirely dedicated to termites have come out (in 2001 and 2011), and they contained limited information on communication processes. In all of the older literature, termites were largely left out of the study of eusocial insect recognition systems. In particular, information on their chemical communication and chemical ecology is scarce. A review by Clément et al. on the chemical ecology of European termites came out in 1988; however, general papers on the topic failed to follow. Fortunately, more recent reviews on chemical communication in social insects have included termites (Richard and Hunt 2013), and some have been entirely dedicated to termite communication (Costa-Leonardo et al. 2009; Costa-Leonardo and Haifig 2010, 2014). In the most recent book on termites (2011), one chapter on communication, written by Bordereau and Pasteels (2011), was included; it dealt with dispersal and foraging pheromones, which are only one small part of termite recognition systems. Recognition is a complex form of chemical communication. Thus, in the course of the social evolution of Isoptera, new exocrine glands were added to those already in existence; these glands are responsible for short- and long-range signaling and recognition. Containing less than twenty exocrine glands, the termite glandular set is rather small and conservative when compared to those of the social Hymenoptera (Gonçalves et al. 2010); the most important glands involved in communication, social regulation, and recognition are the sternal gland, the tergal glands, the labial or salivary gland, and the frontal gland. Many messages are conveyed by volatile signals and can generally be perceived at a distance or require only limited contact. However, physical contact is also a necessary part of numerous behaviors. As a general rule and as in other eusocial insects (ants, wasps, and bees), social recognition in termites is mediated by chemical communication and contact is often required. Indeed, some older publications indicate that contact-mediated signals are involved in termite recognition, with epicuticular compounds, namely cuticular hydrocarbons, playing a primary role. Clément's work (1982a) was one of the first to report this finding. These long-chain hydrocarbons have now been found to be involved in most insect recognition systems (Blum 1987; Singer 1998; Howard and Blomquist 2005; Blomquist and Bagnères 2010). Evidence for their role as recognition cues was discovered 25–30 years ago in ants (nestmate recognition: Bonavita-Courgourdan et al. 1987) and termites (species recognition: Howard et al. 1982a). In some social insects (notably ants), nestmate discrimination is based on variation in cuticular hydrocarbon blends, which are perceived upon antennal contact (by a peripheral organ) (Ozaki et al. 2005); this is also true in termites (Huang et al. 2012a). If, upon contact, the hydrocarbon blend is not recognized as a signal coming from a nestmate, aggressive behavior follows. The various information that is conveyed by hydrocarbons in social Hymenoptera has been well described in recent literature (e.g., Greene and Gordon 2003; Châline et al. 2005; Smith et al. 2009; Eliyahu et al. 2011; Bonckaert et al. 2012; Bos et al. 2012; Van Oystaeyen et al. 2014). Cuticular hydrocarbons play a prominent role in nestmate recognition in both ants (D'Ettore and Lenoir 2010) and termites (Clément and Bagnères 1998). Cuticular hydrocarbons have also been described as primer pheromones maintaining the worker sterility in Hymenoptera (LeConte and Hefetz 2008; Van Oystaeyen et al. 2014), which underscores the multifaceted role of these compounds in social insects. We believe that, particularly in blind insects such as termites, frequent cuticular contact is likely to play a regulatory role in processes such caste epigenetic development. As we conclude our introduction, we wish to point out that, in contrast to the literature on hymenopteran social insects, the termite literature is relatively depauperate, particularly with regards to the topic we are discussing here. It is only over the last decade that a broad range of studies have been published on various aspects of termite biology.

Communication and Social Regulation in Basal Families and Higher Termites

This section reviews communication and social regulation in the most basal termite families, including the less advanced termites belonging to the Rhinotermitidae family, and the most advanced termite family, the Termitidae.

Vibratory Communication

The perception and active production of vibrations are relatively well documented in termites; vibrations are used in a variety of contexts from the exploration of the abiotic environment to social interactions such as alarm and disease signaling. Virtually all termite species demonstrate sensitivity to vibrations propagated by the substrate, and they respond immediately to mechanical disturbances, showing accelerated movement and alarm behavior.

Vibratory Alarm Signals

Body vibration is a widespread behavior observed in various castes in a number of termite species. It is characterized by a series of bursts of movement, each of which comprises several horizontal or vertical body jerks, and is often accompanied by the drumming of the head or the abdomen against the roof (and/or floor) of a gallery or nest (e.g., Stuart 1988; Connétable et al. 1999; Röhrig et al. 1999; Hertel et al. 2011). Vibrations are most often used to propagate alarm signals in response to biotic and abiotic disturbances. Vibratory movements belong to one of three categories: (a) *longitudinal oscillatory movement* (LOM); (b) *vertical oscillatory movement* (VOM) or *head-banging/drumming*; and (c) *complex oscillatory movement* (COM) or *zig–zag movement*, which comprises a combination of horizontal and vertical jerking motions (Stuart 1963; Howse 1965; Leis et al. 1992, 1994). The function of vibratory movements has been studied in detail in *Zootermopsis* (Termopsidae) (Stuart 1963; Howse 1964a, 1965; Stuart 1988; Kirchner et al. 1994) and has been associated with two different types of alarms. First, *specific alarms* involve the local excitement of one or a few individuals. Upon inspecting the source of a disturbance, the alerted termite may perform a LOM and then retreat while laying down an odor trail. When it comes in contact with a nestmate, it may perform a COM and bump into the other termite. The recruited individual or individuals then follow the odor trail to the location of the disturbance. *General alarms* take place when a strong disturbance is perceived at all once by a group of termites. Within the group, a majority of soldiers and a minority of workers will begin to perform a VOM, and the resulting drumming alarm will be perceived by any nestmates nearby. However, it does not elicit a positive feedback response, and the termites receiving the signal will not produce vibrations themselves.

LOMs appear to be ancestral behavioral patterns; they occur as a component of social interactions even in undisturbed groups, in many species and various castes, including reproductives (Sbrenna et al. 1992; Maistrello and Sbrenna 1996; Hertel et al. 2011). Similarly, the directional recruitment seen during specific alarms has been observed in many species, and what is seen in *Zootermopsis* is fairly similar to what is seen in *Macrotermes* or *Nasutitermes* (Traniello and Beshers 1985; Kettler and Leuthold 1995).

In contrast, VOMs accompanied by head-drumming are likely derived signals with considerable evolutionary flexibility. They probably evolved from the widespread LOM behavior, as evidenced by direct observations of LOMs turning into VOMs following strong disturbances and by the structural similarities between LOMs and VOMs within and among species (Röhrig et al. 1999; Hertel et al. 2011). VOMs appear to be absent in the dry-wood termites *Kalotermes* and *Incisitermes*, which live in small colonies whose members remain in close contact (Sbrenna et al. 1992; Hertel et al. 2011). In *Zootermopsis*, drumming behavior occurs in both soldiers and workers, but its alarm propagation capacity is low (Howse 1964a; Stuart 1988; Kirchner et al. 1994) if not absent (Stuart 1963) and elicits no positive feedback. In socially advanced and large colonies, such as those of *Pseudacanthotermes* and *Macrotermes*, the drumming alarm has become a spectacular signaling strategy that allows signal transmission over large distances; head-drumming is a behavior largely restricted to soldiers and elicits an immediate positive feedback reaction from other soldiers (Stuart 1988; Connétable et al. 1999; Röhrig et al. 1999; Hertel et al. 2011). A chain of vibrating soldiers can spread an alarm across a distance of more than a meter in less than a second (Röhrig et al. 1999). The reaction to the drumming alarm is polyethic in advanced termites: soldiers are recruited to drum while workers usually retreat (Stuart 1988; Connétable et al. 1999; Röhrig et al. 1999).

Although termite-produced drumming is audible to humans even at considerable distances, its perception as air-borne sound has not been confirmed in termites (Kirchner et al. 1994; Connétable et al. 1999). Nevertheless, this possibility cannot be ruled out since low-frequency body vibrations may be accompanied by high-frequency sounds produced by stridulatory structures, such as those described in *Kalotermes flavicollis* (Sbrenna et al. 1992). It has also been hypothesized that the synchronized drumming of Macrotermitinae, which evokes a rhythmical hissing, may act as an aposematic signal to warn away predators or as a territorial signal (Howse 1984; Connétable et al. 1999; Röhrig et al. 1999).

Other Functions of Vibratory Communication

Substrate-borne vibrations have also been shown to convey messages other than those of alarm. *Zootermopsis angusticollis* nymphs inform their nestmates of the presence of infections. When exposed to high concentrations of fungal spores, they perform longitudinal and vertical vibrations, seemingly different from the LOMs and VOMs described above. Unexposed termites respond to these vibrations by keeping their distance from infected termites (Rosengaus et al. 1999). The vibrations produced by foraging and feeding can also be used as signals. Drywood termites of the genus *Cryptotermes* choose optimal food sources based on the substrate-borne vibrations produced by their own activity, which are modulated by the size and the other properties of the wood upon which they are feeding (Evans et al. 2005; Inta et al. 2007). At the same time, they are attracted by vibrations produced by their nestmates, and thus the social cohesion of the colony is maintained as a result of the perception of passive signals produced by foraging and wood-chewing (Evans et al. 2007). This same informational cue has been shown to help drywood termites assess the presence of heterospecific competitors in the same block of wood (Evans et al. 2009).

Visual Communication and Recognition

Developed compound eyes are only found in imagoes, future kings and queens, who use them during their dispersal flights. The subsequent search for mates is mediated chemically, and vision plays a negligible or no role (Nutting 1969). The single exception to this rule is the family Hodotermitidae, whose workers possess functional compound eyes. *Hodotermes mossambicus* workers forage at night or during the day in the open air. They employ a more individual style of foraging as opposed to the classical column foraging seen in most other termites. When light conditions are favorable, they visually orient themselves using an internal compass that responds to sunlight or moonlight; simultaneously, they mark their path using pheromones produced by their sternal glands. Optical cues are given preference over chemical cues and are more precise. However, when light conditions are poor and also in the vicinity of their foraging holes, chemical communication dominates and workers are perfectly able to find their way back home solely on the basis of the chemical trail (Leuthold et al. 1976; Heidecker and Leuthold 1984).

Chemical Communication and Recognition

As mentioned before, the dominant role of chemicals in communication, orientation, and recognition is an undisputable characteristic of social insects in general, and termites are no exception. The variety of chemical signals used by termites and their production organs are depicted in Fig. 11.2.

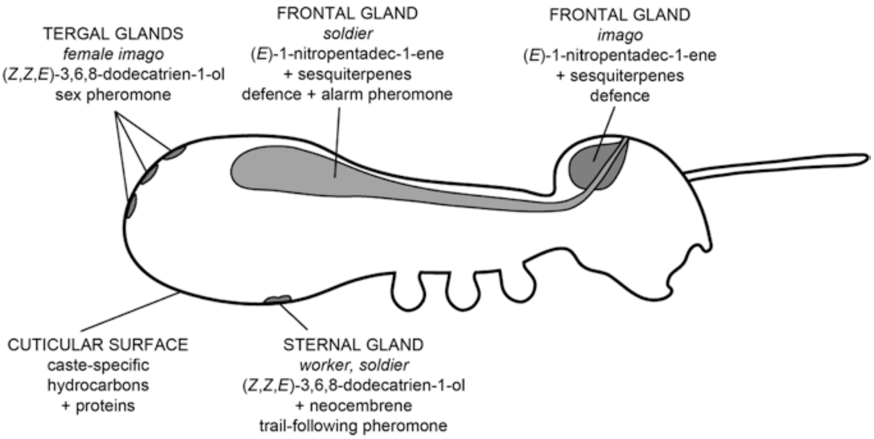


Fig. 11.2 Schematic drawing of a termite body depicting major glandular sources or deposition sites for chemicals used in communication and defense in the termite genus *Prorhinotermes*. The legend shows the chemical identity of the secretion, the function of the secretion (if known), and the caste in which a chemical function has been observed. Based on Piskorski et al. (2007, 2009), Šobotník et al. (2008), Hanus et al. (2009, 2010), and Sillam-Dussès et al. (2009a)

Foraging and Food Marking

Collective foraging in termites has received much attention over the past two decades, including exhaustive reviews by Traniello and Leuthold (2000) and Bordereau and Pasteels (2011). Although termites demonstrate diverse feeding ecologies and nesting habits, their capacity to mark and follow trails is ubiquitous, suggesting a common evolutionary basis in all extant termites. This idea is supported by the universal presence of the sternal gland, as well as by the uniformity of the pheromonal compounds used by evolutionarily distant taxa.

The sternal gland is present in all termite castes and all species studied to date. It occurs as three unpaired glands in the middle of sternites 3, 4, and 5 in the most primitive family, Mastotermitidae. In contrast, it is a single gland on the anterior end of sternite 4 in Termopsidae and Hodotermitidae and a single gland on the anterior margin of sternite 5 in Kalotermitidae and all of the advanced families (Noirot 1969; Quennedey et al. 2008) The glandular secretion is released from the extracellular storage space and from the cuticular fold of the preceding sternite when the walking termite presses its abdomen against the substrate. In Hodotermitidae, the gland is partially evaginated during pheromone deposition (Quennedey et al. 2008).

Foraging consists of two phases: exploration and recruitment. During the search for food, scouts lay down an exploratory trail. Once food has been found, the termites return to the nest using this exploratory trail while simultaneously laying down a recruitment trail that is far more attractive to foragers (Oloo and Leuthold 1979; Traniello 1982). It is difficult to determine whether exploratory and recruitment trails only differ quantitatively, as suggested by the fact that workers lay down a dotted exploratory trail but a continuous recruitment trail, or whether they also differ qualitatively as a result of differences in chemical composition (Affolter and Leuthold 2000). Foraging is often initiated by workers, who are later eventually accompanied by soldiers (e.g., Heidecker and Leuthold 1984; Lys and Leuthold 1991; Reinhard et al. 1997a). However, in many cases, the soldiers themselves precede the foraging columns and patrol foraging trails and sites; this behavior is particularly seen in species that forage freely, without using protective galleries or tunnels (Eisner et al. 1976; Stuart 1981; Traniello 1982; Kaib 1990; Miura and Matsumoto 1998; Connétable et al. 1999). In *Nasutitermes corniger* and *Schedorhinotermes lamanianus*, the soldiers may even serve as scouts and thus actively participate in the exploratory phase: they are the first to search for food and first they attract other soldiers, but mass recruitment takes place only after workers appear on soldier-produced trails (Traniello 1981; Traniello and Busher 1985; Schedel and Kaib 1987; Kaib 1990). The caste specificity of trail-following behavior appears to arise from quantitative differences in trail deposition and pheromone sensitivity between workers and soldiers (Traniello and Busher 1985; Wolfrum and Kaib 1988).

In advanced separate-type termites, feeding strategies are more complex and foraging-related tasks are divided up among two or even three morphs of the different instars and sexes within the worker caste (McMahan 1970; Watson and McMahan 1978; Traniello and Busher 1985; Miura and Matsumoto 1995; Miura et al. 1998). Within the polymorphic worker and soldier castes of *Macrotermes subhyalinus*, major workers are predominately responsible for extranidal activities; until the onset of mass foraging, they repeatedly lay down deposits on the foraging trail while carrying food to the nest (Badertscher et al. 1983; Affolter and Leuthold 2000). In contrast, in *Macrotermes bellicosus*, minor workers are responsible for exploration, recruitment, and gallery construction, while major workers are tasked with foraging (Lys and Leuthold 1991; Gessner and Leuthold 2001). In this case, it has been proposed that the pheromones of major and minor workers are qualitatively different (Gerber et al. 1988; Gessner and Leuthold 2001). In addition, a worker's relative age is correlated with the type of activity it performs; shortly after molting, workers are more likely to perform tasks within the nest, while older workers are more likely to perform foraging-related tasks (Badertscher et al. 1983; Hinze and Leuthold 1999; Hinze et al. 2002).

The chemical diversity of termite trail-following pheromones is surprisingly low; less than ten compounds have been unambiguously identified across more than sixty species from all termite families (Bordereau and Pasteels 2011). In basal families, C_{13}, C_{14}, or C_{18} branched saturated or unsaturated aliphatic alcohols or aldehydes occur, most likely as single-component pheromones. The shift in sternal gland location and morphology seen in the advanced families (Kalotermitidae, Serritermitidae, Rhinotermitidae, and Termitidae) appears to be accompanied by a transition to unbranched mono-, di-, or tri-unsaturated C_{12} alcohols, in some cases occurring in a combination with the diterpene hydrocarbons neocembrene or trinervitatriene (Quennedey et al. 2008; Bordereau and Pasteels 2011). An exception to this rule is the peculiar family Serritermitidae, which uses unsaturated C_{19} ketone as its trail-following pheromone (Hanus et al. 2012). The degree to which termite trail-following pheromones have been conserved across taxa is rather intriguing, because even very distantly related species, such as the one-piece-type *Prorhinotermes* and the very advanced separate-type Macrotermitinae or Nasutiterminae, use the same pheromonal compounds, despite dramatic differences in their nesting habits and ecologies (Peppuy et al. 2001; Sillam-Dussès et al. 2009a, b, 2010). As argued below, trail-following ability seems to have evolved before foraging, and the chemistry of trail-following pheromones has apparently been influenced only minimally by this major transition in feeding ecology.

Some studies have shown that trail-following pheromones have a dual behavioral function in that they promote both ephemeral recruitment and long-lasting orientation (Traniello 1982; Runcie 1987; Affolter and Leuthold 2000). However, most trail-following pheromones identified to date consist of single components. In part, this assertion may be due to past omissions of minor components and soon after the very first two-component trail pheromone was reported (Sillam-Dussès et al. 2009a), a few more multicomponent pheromones emerged (Kotoklo et al. 2010; Sillam-Dussès et al. 2010). Nevertheless, the ability of these components to differentially function as recruitment and orientation cues has yet to be confirmed.

Because they show low chemical diversity, it is hard to understand how trail-following pheromones could serve as species recognition cues. Since no species-specific trail-following compounds have been identified, chemical species specificity, if it exists, may be due to quantitative differences in pheromones or their components (Bordereau and Pasteels 2011). Likewise, there is no evidence that trail-following pheromones can be used to distinguish between competing conspecific colonies.

It would seem that in primitive one-piece-type societies, trail-following abilities would be useless. However, these termites nonetheless have active sternal glands and successfully follow artificial trails (Sillam-Dussès et al. 2009b; Bordereau et al. 2010), which suggests that they may be using trails to orient themselves within the network of galleries located in the wood they inhabit. Trail-following behavior is sometimes considered to have originated from the recruitment associated with specific alarms, during which trail-following pheromone is used to guide the recruited nestmates to the disturbance site. Termites also respond to specific alarms with building behavior, another crucial activity in the construction of covered galleries by foraging species (Stuart 1967; Traniello and Leuthold 2000). Thus, sternal gland presence, trail-following ability, and building behavior appear to be good preadaptations for the evolution of external foraging and a true worker caste. This assertion is supported by the transitional situation of the one-piece-type termite *Prorhinotermes*: it is able to leave the nest and search for new food sources during food shortages using foraging trails and covered galleries (Rupf and Roisin 2008). At the same time, as argued below, trail-following behavior is also thought to have originated from the ancestral behaviors of airborne mate attraction and trail-mediated pair cohesion. Observations of the foraging behavior of the primitive termite *Mastotermes darwiniensis* support this hypothesis; unlike all other termites, which forage in columns, *M. darwiniensis* workers proceed either alone or in tandems (Sillam-Dussès et al. 2007). Thus, the most parsimonious scenario describing the evolution of trail-following is as follows: mate attraction and tandem behavior in solitary ancestors, then alarm recruitment in primitive societies, and finally external foraging (Rupf and Roisin 2008; Bordereau and Pasteels 2011).

Once food has been located, termites often tend to aggregate at that spot and feed in groups. It has been shown in a number of species that aggregation is mediated by the saliva secreted from the labial (salivary) glands (Kaib and Ziesmann 1992; Reinhard and Kaib 1995; Sillam-Dussès et al. 2012). Hydroquinone has been identified as the active chemical in the saliva and is thought to be the food-marking pheromone and a general phagostimulant in termites (Reinhard and Kaib 2001b; Reinhard et al. 2002).

Pheromone communication is also used during building, which has reached its most complex form in the fungus-growing termites of the genus *Macrotermes*. The coordinated action of thousands of workers during the construction of spectacular mounds is modulated by the presence of previously built structures via stigmergy, or self-organized mass action (Grassé 1959a, b; Bonabeau et al. 1997). *Macrotermes* workers use soil pellets that are cemented together using salivary secretions. Freshly deposited pellets are attractive to workers and stimulate them to add new pellets. According to the shape and size of the structure already in place, the construction continues vertically (pillar construction) or laterally (lamellar construction). This building behavior is coordinated by a "cement pheromone", whose chemistry is unknown; it is secreted by workers during pellet deposition and combined with trail-following pheromone from the sternal gland (Bruinsma 1979). It is apparent that a tight link between trail-following pheromones and building exists in many other termite species, including lower termites, namely during the construction of galleries along foraging trails and repairs; builders are recruited to damaged nest areas using a pheromone trail (Stuart 1967).

Mate Attraction and Recognition

Long-range, short-range, and contact chemical cues are used by future kings and queens in mate attraction, recognition, and choice, following their dispersal flights from their natal nests. Typical post-flight behavior consists of a sequence of activities: long-range attraction, pair formation, and tandem promenade of the partners to the future nesting site. Sex pheromones, also known as sex-pairing pheromones (Bordereau and Pasteels 2011), are produced by the sternal glands, posterior sternal glands, tergal glands, or a combination thereof. While all castes have sternal glands, which are also used for trail marking, only the imagoes of some species possess posterior sternal glands and tergal glands (Bordereau et al. 2002; Quennedey et al. 2004). In the basal families, both males and females (Termopsidae; Bordereau et al. 2010) or exclusively males (*H. mossambicus*;

Leuthold and Bruinsma 1978), produce sex pheromones. In the more advanced families, only the females call the males (Bordereau and Pasteels 2011). Once a pair has formed, the male usually follows the female during the search for a suitable nesting site in a “tandem run”, during which the male touches the female’s posterior abdomen with his antennae and mouthparts. In some species, the female may use her sternal gland to mark the trail during the tandem run to prevent accidental separation. The mating itself takes place only after the nesting site has been chosen and the future royal chamber has been built (Nutting 1969; Bordereau and Pasteels 2011).

In spite of the fact that the chemistry of sex pheromones is less well known than that of trail-following pheromones, many important characteristics common to both these modes of communication are obvious. First, the sex pheromones demonstrate a low chemical diversity and are mostly composed of single components. Second, the sex pheromones identified in individual species often also act as trail-following pheromones or are structurally very similar. Thus, branched C_{13} or C_{14} alcohols and aldehydes, unbranched unsaturated C_{12} alcohols and diterpenes neocembrene and trinervitatriene occur as sex pheromones, with just one additional molecule, the sesquiterpene alcohol (*E*)-nerolidol, being a sex pheromone component unrelated to the trail-following pheromones (Bordereau and Pasteels 2011; Bordereau et al. 2011). When compared with trail-following communication, the specificity of mate attraction results either from (a) different major components, (b) different, and sometimes much higher, concentrations of the sex pheromone, or (c) the occurrence of one or more additional, minor components (Bordereau and Pasteels 2011). The widespread use of the sternal gland in courtship behavior as well as the frequent occurrence of the same pheromone (or components) in both contexts support the hypothesis that the trail marking is probably derived from the mate attraction of termite imagoes during dispersal (Traniello and Leuthold 2000; Bordereau and Pasteels 2011).

Reproductive isolation of sympatric species was logically thought to be maintained by differences in the chemical composition of the sex pheromones, or perhaps by the addition of species-specific minor components to the shared major component. While this appears to be true in some species (e.g., Peppuy et al. 2004; Bordereau et al. 2011), in others only pheromone quantities differ between congenerics (Bordereau et al. 1993, 2010; Connétable et al. 2012). As a result, reproductive isolation is probably maintained by other mechanisms, such as the differential timing of the dispersal and contact species recognition cues (Connétable et al. 2012), which are further discussed below.

Sex pheromones advertise the presence of the opposite sex but probably do not drive partner choice, which is expected to occur in termites given the long-term biparental care provided by kings and queens to their offspring and the strict lifelong monogamy characteristic of many termite species. Indeed, more and more experimental evidence suggests that the pairing of males and females is controlled rather than random and mates are chosen based on numerous criteria, such as partner relatedness (Shellman-Reeve 2001), size and body mass (Shellman-Reeve 1999; Kitade et al. 2004), and level of heterozygosity (Husseneder and Simms 2008).

Chemical Alarm

Chemical alarms serve to initiate local recruitment by means of short-range attractants. Secretions produced by the frontal glands of soldiers are involved and thus chemical alarms are only found in the Rhinotermitidae, Serritermitidae, and Termitidae. Alarm pheromones are included in the blend of defensive chemicals and are released when excited and/or fighting soldiers discharge their frontal glands. It is to note that today we don't know any work on chemical alarm system on soldierless species. This type of alarm initiation has been observed in a few rhinotermitids, such as *Prorhinotermes*, *Schedorhinotermes*, and several *Reticulitermes* species, as well as numerous termitids, including many species belonging to Nasutitermitinae (Šobotník et al. 2010). All termite alarm pheromones confirmed as yet were identified to be of a terpenoid structure. Sesquiterpene hydrocarbon (E,E)-α-farnesene has been described as alarm pheromone in *Prorhinotermes canalifrons* (Šobotník et al. 2008). Monoterpene hydrocarbons elicit alarm in Nasutitermitinae, namely α-pinene in *Nasutitermes princeps* (Roisin et al. 1990) and a blend of several monoterpenes in *N. rippertii* (α-pinene, limonene and β-pinene) and *N. costalis* (3-carene, limonene, β-pinene, α-pinene, terpinolene) (Vrkoč et al. 1978). The role of these compounds in communication is supported by their enantiomeric purity, which is a common feature of pheromones (Lindström et al. 1990; Valterová et al. 1992, 1993).

The reaction elicited in nestmates by alarm pheromones is caste specific: soldiers are always attracted to the odor source while workers are attracted in some species while in others they escape. They are sometimes attracted to the disturbance site only after a certain amount of time has passed, and they eventually participate in the defense of the colony, either by fighting or by building and depositing fecal material on enemies (Eisner et al. 1976; Stuart 1981; Traniello 1981; Kaib 1990). An alarm signal mediated by worker feces has been observed in *H. mossambicus* (Wilson and Clark 1977).

Nestmate Recognition and Agonism

Theories regarding the evolution and maintenance of eusociality predict that subtle mechanisms are involved in nestmate and kin recognition in social insects (Breed 1987), resulting in colony cohesion on the one hand and agonistic interactions between non-relatives, intercolonial hostility, and territoriality on the other hand. Indeed, termites have aggressive encounters with heterospecific competitors, and agonistic, often lethal interactions between conspecifics from different colonies frequently take place—these ultimately lead to the territorial isolation, usurpation, or death of the defeated colonies (reviewed in Thorne 1982; Thorne and Haverty 1991; Shelton and Grace 1996; Clément and Bagnères 1998). Depending on the context, various castes, namely soldiers, workers, or reproductives, may display aggressive behavior.

Agonistic interactions may occur as early as during colony founding. In *H. mossambicus*, the onset of aggressiveness towards conspecific reproductives can be observed as soon as the royal pair is established (Nel 1968; Hewitt et al. 1972). Early-stage competition is particularly intense in one-piece-type termites. Founding reproductives of *Zootermopsis nevadensis* cooperatively defend their nest sites in wood against other pairs of reproductives and/or unpaired newly flown reproductives (Shellman-Reeve 1994, 1999). Conflicts take place as the colonies develop and compete for food and space within a single log, and these conflicts often result in the death of one or both primary reproductives; colonies may subsequently merge and behave as a single unit, and the lost reproductives are replaced by neotenic reproductives (Johns et al. 2009). It has been suggested that the occurrence of fertile soldiers in Termopsidae is an adaptation of the future potential replacement reproductives for such conflicts (Thorne et al. 2003). Colony fusions that result from conflicts and the elimination of primary reproductives also occur in other one-piece-type termites, such as *C. secundus* (Korb and Schneider 2007; Korb and Roux 2012) and *K. flavicollis* (Luchetti et al. 2013a). In contrast, the rare cases of cooperative colony founding are largely restricted to the higher termites (Hacker et al. 2005; Hartke and Rosengaus 2013).

In separate-type termites, aggressive encounters between foraging parties are common and both soldiers and workers participate in the agonism. In soldierless Apicotermitinae (Sands 1982) and Hodotermitidae, which forage without soldiers (Nel 1968), workers are particularly aggressive; however, even in the higher termites, workers are active fighters even though they are protected by numerous soldiers (Thorne 1982; Leponce et al. 1996; Jmhasly and Leuthold 1999a). Intercolonial interactions can involve thousands of individuals and may wipe out entire colonies (Levings and Adams 1984; Leponce et al. 1996) or, more often, lead to the spatial separation of territories. Territory boundaries are dynamic and defined by repeated encounters between neighboring colonies, and the former zones of contact are lined with dead bodies generated by past conflicts (Darlington 1982; Levings and Adams 1984; Jmhasly and Leuthold 1999b). When two colonies interact, whether more or less aggressively and with or without ensuing mortality, intensive building activities often follow. The acts of building and depositing materials result in the divergence and displacement of foraging trails (Levings and Adams 1984; Leponce et al. 1996), thus preventing or resolving conflicts, both within pieces of wood as well as in subterranean tunnels and aboveground covered galleries (Darlington 1982; Pearce et al. 1990; Schuurman and Dangerfield 1995; Jmhasly and Leuthold 1999b, c). The intensity of agonism between conspecific colonies is highly variable. While, in most cases, overt aggression results from the encounter, sometimes aggression is limited or absent. Agonism varies among species, colonies, and nests (Jmhasly and Leuthold 1999b; Adams et al. 2007), as well as among individuals; therefore, a colony's response may change over time as the most aggressive individuals are killed off in conflicts (Leponce et al. 1996).

A few studies have found a direct correlation between the level of aggression and the genetic distance between colonies, such as in *Schedorhinotermes* *lamanianus* (Husseneder et al. 1997, 1998) or *Microcerotermes arboreus* (Adams 1991); however, others have not found such a relationship (e.g., Husseneder and Grace 2001). Low genetic diversity due to the "founder effect" may explain reduced agonism in introduced populations, resulting in open societies with a tendency to form supercolonies (Perdereau et al. 2010a; also see below). However, in contrast, increased genetic diversity appears to be responsible for the low level of aggressiveness in colonies founded cooperatively by several unrelated reproductives (pleometrosis), as observed in *N. corniger* (Adams et al. 2007) and possibly also in *M. bellicosus* and *M. michaelseni* (Schuurman and Dangerfield 1995; Jmhasly and Leuthold 1999a; Hacker et al. 2005).

The spatial distance between colonies has been examined in a few studies that have aimed to test the "dear enemy" hypothesis (or the "neighbor-stranger" effect), which predicts that frequently encountered colonies will be attacked less often than non-neighbors. While this hypothesis has been supported in some cases (e.g., *Macrotermes falciger*, Kaib et al. 2002), several other cases suggest that distance does not influence the pattern of aggressiveness (Leponce et al. 1996; Jmhasly and Leuthold 1999a; Adams et al. 2007; Marins and de Souza 2008), and in fact, the opposite trend has been observed in *N. corniger* (Dunn and Messier 1999).

The aggressiveness of colonies may also vary with seasonal and geographical factors. During some seasons of the year and in some parts of a species' range, colonies may behave as open societies, demonstrating low levels of agonism, allowing colony fusions, permitting fluctuations of individuals, and tolerating numerous reproductives; in contrast, during other seasons and in other locations, colonies may remain closed familial units that are isolated by means of aggressive interactions (Clément 1986; Kaib and Brandl 1992). Instantaneous levels of aggression are also fine-tuned based on the actual caste composition of the colony at the site of the conflict. *Zootermopsis* pseudergates are more aggressive towards intruders when they are close to reproductives or when only a few soldiers are around (Ishikawa and Miura 2012). When there is a high proportion of nymphs in a colony, the level of agonism may be decreased, which facilitates the colony's acceptance of and potential fusion with a conspecific colony that has a lower proportion of nymphs. This type of situation may occur because it is beneficial for the host colony: it recruits more workers to care for the nymphs (Matsuura and Nishida 2001). Nymph-containing colonies of *Macrotermes gilvus* and *M. carbonarius* always reject reproductives, while nymphless colonies may eventually accept them (Neoh et al. 2012). The adaptive value of this acceptance is questionable, as are a few other examples of low levels of intraspecific agonism.

Chemical Cues Involved in Nestmate Recognition

The recognition process, which leads to the acceptance or rejection of an individual as a nestmate or non-nestmate, appears to rely on direct contact involving the antennae and/or palps that takes place during the behavioral inspection sequence (Clément 1981). The blend of cuticular hydrocarbons (CHCs) contained in the hydrophobic epicuticular layer most likely serves as one of the major contact recognition cues. CHCs have been receiving more and more attention for their role as recognition cues in social hymenopterans, and their significance in termites is now being studied as well. Summaries of the chemistry and biology of CHCs, with an emphasis on social insects, have been provided in several reviews and review chapters (e.g., Blomquist et al. 1998; Clément and Bagnères 1998; Howard and Blomquist 2005); the two topics have also been the subject of an entire book (Blomquist and Bagnères 2010).

CHCs are a rich mixture of straight-chain, methylated, saturated, and unsaturated hydrocarbons. The expected low volatility of contact recognition cues matches well with the chain lengths of CHCs, which usually range from over 20 to 40 carbon atoms when analyzed using gas chromatography (the predominant technique) but can exceed 70 carbons when different analytical tools are employed (Cvačka et al. 2006; Sutton et al. 2013). Generally, CHC patterns differ qualitatively among individual species and quantitatively among populations and colonies of the same species (van Zweden and d'Ettorre 2010). This finding, which dates back to late 1970s and early 1980s (Howard et al. 1978; Blomquist et al. 1979) has paved the way for CHC analysis to be used to identify cryptic species and to be employed in studies on the biogeography of populations and species, including termites (reviewed in Bagnères and Wicker-Thomas 2010). In addition to the extensive use of CHCs as taxonomic markers in subterranean termites (see below), CHC analysis has also been used to distinguish among species of lower termites, such as *Zootermopsis* (Haverty et al. 1988; Korman et al. 1991), *Glyptotermes* (Takematsu and Yamaoka 1997), and *Cryptotermes* and *Incisitermes* (Haverty et al. 2000), as well as among species of higher termites, such as *Nasutitermes* (Howard et al. 1988), *Odontotermes* (Bagine et al. 1990; Thorne and Page 1990; Kaib et al. 1991), *Macrotermes* (Bagine et al. 1994), and *Drepanotermes* (Brown et al. 1996a), among others. Using CHCs to distinguish species has some limitations; for instance, within *Macrotermes*, dramatic differences in CHC phenotypes do not necessarily translate into differences in species identity (Kaib et al. 2002; Marten et al. 2009). Nevertheless, CHC analysis continues to serve as a complement to the genetic tools predominately used in termite taxonomy.

Support for the hypothesis that CHCs serve as nestmate recognition cues in termites has accumulated over the past decades, mainly in the form of indirect correlative observations that show that differences in CHCs among colonies are correlated with aggression levels or genetic distances. A good match between CHC patterns and either aggression or genetic distance or both has been observed in a number of subterranean termites (e.g., Dronnet et al. 2006; see below), a few lower termites, such as *Zootermopsis* (Haverty and Thorne 1989; Korman et al. 1991), and some higher termites, such as *Macrotermes* (Kaib et al. 2002, 2004). Finally, colony-specific CHC patterns have been observed to be transmitted via termite feces, which may therefore potentially serve as a signal source in some termites (Lewis et al. 2010). Direct evidence for the role of CHCs in recognition has been found in some intermediate termites (see later).

Another source of intercolonial chemical variability in addition to CHC blends is the defensive chemicals produced by the frontal glands of soldiers. Interspecific differences in frontal gland chemistry are well known (Šobotník et al. 2010) and can be used as chemotaxonomic markers along with CHCs (e.g., Bagnères et al. 1990a). Conspicuously different defense compound chemotypes have also been observed within species (e.g., Valterová et al. 1989) or even among colonies with the same CHC chemotype (Šobotník et al. 2010; Krasulová et al. 2012), which may reveal another level of intraspecific polymorphism that can be used when disentangling the relatedness and dispersal history of populations. Whether defense compound chemotypes are also used by the termites themselves in intercolonial recognition is unknown, but it is a relevant hypothesis that remains to be tested.

Caste Recognition and Social Regulation

Mutual recognition of caste identity within the colony is vital to the effective division of labor, the coordination of social activities, and the care of dependent immatures, soldiers, and reproductives. Caste recognition involves an instantaneous contact event that is followed by mutual antennal inspection. Therefore, once again, non-volatile chemical signatures on body surfaces are likely to serve as recognition cues and CHCs may potentially be involved. Indeed, several studies focusing on intercaste differences in CHC profiles have detected more or less pronounced caste specificity in CHC signatures, which would allow caste discrimination based on quantitative patterns of CHCs in lower, intermediate, and higher termites (Howard et al. 1982a; Haverty et al. 1988, 1996; Bagnères et al. 1990b, 1998; Brown et al. 1996b; Sevala et al. 2000; Klochkov et al. 2005). Quantitative caste-specific CHC signatures are neither conserved nor consistent across all colonies of a given species; instead, they change from one colony to the next (Haverty et al. 1988). In spatially distant colonies of *Drepanotermes perniger*, one specific compound has been observed to be overrepresented in larvae and young nymphs (Brown et al. 1996b). The specificity of the chemical signature of immature termites is also evidenced by repeated observations that immatures are seldom attacked in intercolonial conflicts and are therefore recognized and tolerated, or only eventually non-recognized as being foreign (Traniello and Beshers 1985; Thorne and Haverty 1991). The mechanism of caste-specific CHC divergence in genetically identical nestmates is not well understood. Some observations suggest that the common pool of CHCs in the hemolymph differentiates into caste-specific cuticular profiles during CHC externalization due to the regulatory action of hemolymph transport proteins, lipophorins (Sevala et al. 2000). However, all of these findings provide only indirect evidence of the possible role of CHCs in caste recognition; to date, no empirical studies have clarified the mechanism at work.

Information on caste ratios is of crucial importance in the social homeostasis of the colony. Species- and context-dependent optima in the ratio of soldiers (Haverty 1977) are regulated (stimulated or inhibited) by the proportions of other castes. It has been well documented that the differentiation of soldiers can be stimulated by the presence of reproductives (Bordereau and Han 1986) or nymphs (Lenz 1976). Caste inhibition is a regulatory feedback mechanism that is complementary to caste stimulation. The presence of soldiers has frequently been shown to inhibit the formation of additional soldiers (e.g., Miller 1942; Springhetti 1970; Nagin 1972; Lenz 1976; Renoux 1976; Haverty 1979; Haverty and Howard 1981; Lefeuve and Bordereau 1984; Okot-Kotber 1985; Okot-Kotber et al. 1991). Even in incipient colonies, the first soldier(s) efficiently inhibit(s) the production of other soldiers, often for up to one or two years (e.g., Castle 1934; Light and Weesner 1955; Grassé and Noirot 1958). It is thought that primer pheromones, produced by the soldiers present, are responsible for inhibition and that their transmission requires direct contact between the soldiers and the undifferentiated individuals (Springhetti 1970; Okot-Kotber 1985), which implies that the pheromones would have low volatility.

Inhibitory primer pheromones are hypothesized to come from the frontal glands of soldiers. In *Schedorhinotermes lamanianus*, the primer pheromone is thought to be tetradec-1-en-3-one, which is produced by the frontal gland. However, its inhibitory activity was found to be accompanied by high mortality; as a result, the decrease in soldier production cannot be separated from the toxic effect of the compound (Renoux 1976). The inhibitory effect of soldier body extracts and frontal gland extracts on the production of additional soldiers has also been clearly demonstrated in *Nasutitermes lujae* (Lefeuve and Bordereau 1984). Significant progress has been made towards understanding the role of the frontal gland in regulating soldier production in *Coptotermes* and *Reticulitermes*, as discussed below. However, these results cannot be generalized to all termites because only the advanced lineages possess frontal glands. Thus, it would seem that two fundamentally different methods of caste inhibition have evolved in termites. For instance, soldier head extracts have been shown to inhibit soldier differentiation in *C. secundus*, a species without a frontal gland, which suggests that the source of the inhibitory compound is located in the head (Korb et al. 2003). Therefore, another source for the soldier's primer pheromone must exist; for instance, the unicellular glands on the surface of soldiers' heads are a possibility (Grassé 1986).

Recognition of Reproductives, Reproductive Status, and Queen Dominance

The reproductive division of labor between the minority of breeders and the sterile majority of helpers requires that nestmates effectively recognize the presence of reproductives in a variety of contexts. First, reproductives convey that they are present and fertile, thus maintaining their reproductive dominance and inhibiting the development of neotenic reproductives (primer pheromone function). Second, kings and queens signal their presence to elicit tending behavior, such as grooming, feeding, defense, and egg care (releaser pheromone function; see Fig. 11.3). These two types of signaling, referred to as fertility signals for simplicity's sake, are not mutually exclusive; based on our current understanding, there

Fig. 11.3 A physogastric primary queen, a neotenic king, soldiers, and workers of the neotropical higher termite *Silvestritermes holmgreni*. Note the worker removing the eggs laid by the queen. Photo by R. Hanus

is no evidence that these different effects are the consequences of discrete signals as opposed to a single, multifunctional signal emitted by mature or maturing reproductives.

Traditionally, the control exerted by reproductives over the reproductive potential of their nestmates has been considered to be inhibition or manipulation. The social aspects of this inhibition were described in pioneering studies on *K. flavicollis*, *Zootermopsis*, and *Reticulitermes* (Pickens 1932; Light 1944; Grassé and Noirot 1946; Lüscher 1956) and have been situated in the classical model of social control: king(s) and queen(s) inhibit, in concert, the formation of neotenics using a putative, non-volatile, inhibitory chemical substance, which is spread among nestmates by mutual contact, grooming, and/or trophallaxis (Lüscher 1961). When this inhibitory signal is decreased or absent, neotenics form from the immature termites and culled down to a species-specific optimum by siblicidal fights and cannibalism (Lüscher 1952; Nagin 1972; Lenz 1985). Over the long span of research on the topic, several hypotheses related to the mechanisms of reproductive control have been advanced. For instance, it has been proposed that the inhibitory substance is transmitted by proctodeal feeding by reproductives (Lüscher 1955), a hypothesis that has been rejected several times (Nagin 1972; Stuart 1979; Greenberg and Stuart 1980, 1982). It has also been suggested that the substance is secreted by the mandibular gland or accessory glands (Lebrun 1972; Greenberg and Plavcan 1986), via the cuticle (Lüscher 1974; Bordereau 1985; Šobotník et al. 2003) or that inhibition is due to the pheromonal action of the juvenile hormone (Lüscher 1972; Myles and Chang 1984). None of these hypotheses have received decisive support, and the major mystery of termite biology has long remained unresolved.

The past few years have brought new insights and ideas to the field of termite reproductive control. It is now thought that non-reproducing individuals in insect societies are not necessarily helpless victims of manipulation, but rather decision-making subjects that choose the best option in terms of inclusive and exclusive fitness benefits. The signals emitted by functional reproductives can therefore be viewed as honest signals, which announce the presence of fertile individuals (Keller and Nonacs 1993) and prevent overt conflicts over reproduction (Ratnieks et al. 2006). In eusocial hymenopterans, such fertility signals have repeatedly been ascribed to CHCs (Monnin 2006; Peeters and Liebig 2009; van Zweden and d'Ettorre 2010; Van Oystaeyen et al. 2014). In 2009, two independent studies on *Cryptotermes* and *Zootermopsis* reported that the CHC signatures of functional neotenics demonstrate both quantitative and qualitative specificity, and the studies concluded that, in termites, CHCs may also be involved in fertility signaling and/or reproductive control (Liebig et al. 2009; Weil et al. 2009a). Interestingly, in both species, reproductives were characterized by the occurrence of long-chain and branched alkanes or alkenes, which are compounds that are also present in the fertility signals of some social Hymenoptera. Furthermore, king- and queen-specific peptides and proteins were recently found on the body surfaces and in the anal secretions of reproductives of *Prorhinotermes simplex*, *Reticulitermes flavipes*, and *K. flavicollis*, and they were present in quantities that correlated with estimates of the reproductives' fertility (Hanus et al. 2010). Along with the search for fertility-related chemicals, molecular biology has also recently provided insight into differential gene expression by neotenic queens and sterile individuals in *Cryptotermes*; these findings have thus helped pinpoint specific genes that are linked with reproductive status (Weil et al. 2007). Among these queen-specific genes, three are conserved across several species of the genus (Weil et al. 2009b). Silencing one of these genes (*neofem2*) in queens of *C. secundus* resulted in an increase in aggressive behavior among sterile individuals, just as if the colonies had become queenless (Korb et al. 2009). The authors concluded that this gene is responsible for controlling the reproduction of sterile immatures. This gene appears to be homologous to the β-glycosidase gene and thus could have evolved from having an ancestral role in cellulose digestion to having a role in signaling; for instance, it may release signaling molecules from sugar complexes. Unfortunately, the long-term impact of *neofem2* silencing on the reproductive potential of colony members could not be studied. Additionally, the putative pheromone signals involved in the proposed β-glycosidase mechanism and their ultimate origin are as yet unknown. In 2010, the search for termite royal pheromones resulted in the identification of the first queen-produced primer pheromone regulating neotenic differentiation in the Japanese termite *Reticulitermes speratus* (Matsuura et al. 2010; see also the second part of this chapter for details). These findings represent great progress in our efforts to understand the regulatory processes present in termite colonies and show that the queen pheromone has multiple impacts on the maintenance of social homeostasis (Bussell and Vosshall 2010; Matsuura 2012).

The need for a volatile long-range signaling of the presence of reproductives is obvious in colonies of higher termites, which sometimes contain millions of individuals. Indeed, queens in higher termite species have previously been found to release volatile compounds. Any observer opening a termite royal cell housing a large, physogastric queen would immediately notice the dramatic impact that the queen's presence has on the behavior of the sterile castes (see Fig. 11.3). The queen is surrounded by numerous workers, and her entire body is continuously groomed; workers pay particular attention to the posterior part of her abdomen, and along with removing the eggs she lays, they lick the liquid secretions released by her anus and/or gonopore. Simultaneously, workers feed the queen with their salivary fluids. The attraction the queen exerts on the workers, the result of which is analogous to the retinue that forms around the honey bee queen, has been observed by numerous researchers in a number of termite species (e.g., Grassé 1986). The production of a volatile "building" pheromone by *Macrotermes* queens was postulated a long time ago, and it has been suggested that it regulates the building behavior of workers as they construct the royal chamber around the physogastric queen (Bruinsma 1979; Bonabeau et al. 1998). Similarly, primary queens of *Nasutitermes tasakagoensis* have been reported to release volatiles of yet unknown function (Himuro et al. 2011).

Kin Recognition and Nepotism

Since monogamy predominates in the early stages of colony foundation and persists for the whole existence of the colony in many species, the potential for kin-biased behaviors, such as nepotism, is limited and has seldom been studied. In colonies of *C. secundus* that arise from the fusion of two colonies, termites prefer to cooperate and interact exclusively with their relatives during unfavorable conditions (i.e., food shortages) (Korb 2006). In contrast, no evidence of nepotism has been observed in multiple-queen colonies of *N. corniger* in terms of the care provided to related and unrelated queens by workers (Atkinson et al. 2008). Kin-biased foraging has been reported in polygamous colonies of *Schedorhinotermes lamanianus*; workers were grouped into foraging parties based on kinship (Kaib et al. 1996).

Communication and Social Regulation in Intermediate Termites

In this section, we review communication and social regulation in the three intermediate termite genera: *Reticulitermes*, *Heterotermes*, and *Coptotermes*. In the most parsimonious phylogenetic tree inferred from mitochondrial genes (Lo et al. 2004), the three genera cluster together on a branch that includes the advanced termites (Inward et al. 2007a; Engel et al. 2009; Legendre et al. 2013). All three genera feed on dead wood. Some authors place the genera in two different subfamilies: the Coptotermitinae, which contains *Coptotermes*, and the Heterotermitinae, which contains *Reticulitermes* and *Heterotermes*. They all have a subterranean life style and, for this reason, similarities in their biology, including communication and recognition, are to be expected. These termites, like most other termite species, have only a single caste that demonstrates positive phototaxis: the alates, which have well-developed compound eyes and ocelli, move towards light sources during their dispersal flights. The other castes demonstrate light sensitivity that results in negative phototaxis (Hertel et al. 2011). The other types of communication used by the intermediate termites depend more on the particular life style and evolutionary history of the species.

Vibratory Communication

Like most other pterygote insects, termites can also perceive substrate-borne vibrations with a complex chordotonal organ, the subgenual organ, located in their tibias (Howse 1964b). Even if termites all have cryptic life styles, mechanical communication (called vibroacoustic communication in Hunt and Richard 2013) is not universally used across all species. Jerking or whole-body movement is performed by *Coptotermes* and *Reticulitermes* when they are disturbed, and this behavior is generally accompanied by mandible spreading. However, head-drumming is not a general feature of all intermediate termite species. Both workers and soldiers perform this behavior, generally considered to be an alarm behavior (Hertel et al. 2011), but the presence of workers is crucial in this form of communication (Reinhard and Clément 2002).

Chemical Communication and Recognition

As said before, in the whole of the living world, communication takes place first and foremost via chemical means, as already stated. In animals, most chemical communication takes an olfactory form (and also occasionally a gustatory form). It is clear that chemical communication is the primary tool used by social insects, and thus in intermediate termites, to recognize and be recognized by congeners.

Communication in Foraging Behavior

Foraging is one of the primary collective behaviors that is mediated by chemical communication. Intermediate termites are separate-type termites, meaning they have multiple nest sites (Abe 1987, 1990). Foraging involves a division of labor, with workers serving as the main foragers. They excavate tunnels and galleries in their search for food and then recruit nestmates using semiochemicals (Runcie 1987). The main trail-following pheromone described in *Reticulitermes* is (*Z,Z,E*)-dodeca-3,6,8-trien-1-ol, which is released by the sternal gland (Saran et al. 2007; Bordereau and Pasteels 2011). Building activity, which is a non-centralized cooperative behavior, is considered to be one of the best examples of stigmergy, as indicated earlier, and involves a stimulus–response pattern. In addition to the sternal gland, the salivary glands likely play a role in releasing chemicals that mediate building activity; however, to date, no such pheromones have been described. *R. speratus* shows colony-specific architectural variation in shelter tube construction, which reflects intercolonial differences in foraging strategies. These differences may have significant fitness consequences depending on how food is distributed in the environment (Mizumoto and Matsuura 2013). In *R. flavipes*, most of the workers demonstrate feeding site fidelity, which suggests that they may be leaving chemical markers in galleries and nodes, depending on the task they are performing. Observations of termite foraging and travel between resources suggest that communication is uninterrupted within the subterranean polydomous network (Long and Thorne 2006).

Feeding behavior is influenced by semiochemicals released by the labial gland, both in *Coptotermes* and *Reticulitermes* (Reinhard et al. 1997a, b; Reinhard and Kaib 2001a; Casarin et al. 2003); these chemicals are called phagostimulants. Hydroquinone, the primary phagostimulant, must continuously be reapplied (Reinhard and Kaib 2001b). This compound may play a role in regulating food consumption rate, depending on its concentration over time. Furthermore, labial gland extracts are not appealing to soldiers, but glandular secretions could modulate soldier recruitment (Casarin et al. 2003).

Communication in Defense and Alarm Behavior

Defense is another collective behavior that involves chemical communication. This category includes both alarm and defense (protection against predators and intraspecific competition) mechanisms. The defense glands found in the heads of soldiers release the semiochemicals involved in both. As mentioned in the previous section, alarms can either be general, i.e., elicited by the vibratory movements of soldiers liberating frontal gland secretions, or specific, i.e., elicited by physical contact between alerted and recruited termites (Šobotnik et al. 2010). In intermediate termites, defensive secretions are released from the frontal gland and combined with mechanical defense-mandibular opening and biting. Soldiers, and often also the workers, are attracted by the volatiles from the soldier frontal gland and perform a series of alarm behaviors (Reinhard et al. 2003; Nguyen et al. 2011). In *Reticulitermes grassei*, the alarm reaction is elicited by the sesquiterpene hydrocarbon γ-cadinene, in *R. banyulensis* by the diterpene alcohol geranyllinalool, in *R. flavipes* by the monoterpene hydrocarbons α-pinene, β-pinene and limonene, and diterpene alcohols geranyllinalool and geranylgeraniol, and finally in *R. lucifugus* by the sesquiterpene hydrocarbons germacrene A, germacrene

C, β-selinene, γ-selinene, γ-cadinene and the diterpene alcohol geranyllinalool (Quintana et al. 2003).

In *Coptotermes*, secretions are composed of various compounds such as simple hydrocarbons, aromatic compounds, ketones, alcohols, and ceramides that may act as fumigants (Chen et al. 1998, 1999; Zhang et al. 2006; Ohta et al. 2007), and the presence of *Coptotermes formosanus* soldiers has been shown to inhibit the formation of additional soldiers (Park and Raina 2003, 2005). This primer effect produced by the soldiers requires direct contact between the soldiers and the undifferentiated individuals (Dong et al. 2009). Interspecific variation in the terpenoid content of *Reticulitermes* frontal gland secretions was observed by Quintana et al. (2003), and the chemical components present in *R. flavipes* frontal gland secretions have been particularly well described (Zalkow et al. 1981; Bagnères et al. 1990a; Tarver et al. 2009). It has also been shown that the terpenoids released by *Reticulitermes* soldiers have a regulatory effect on the differentiation of soldiers as seen in *Coptotermes* (Park and Raina 2003, 2005). This primer effect (which is distinct from the different releaser effects described at the beginning of the paragraph) is attributed to two sesquiterpenes, namely γ-cadinene and its aldehyde, which enhance the effect of the juvenile hormone (JH) on *R. flavipes* soldiers (Tarver et al. 2009, 2010, 2011). Two hexamerin proteins, which are controlled by two genes (*Hex-1* and *Hex-2*), suppress JH-mediated differentiation of workers into soldiers (Zhou et al. 2006); JH and soldier head extracts have opposing effects on several regulatory genes but have few regulatory effects on the gut microbiome (Sen et al. 2013). Watanabe et al. (2011) obtained other results in *R. speratus*. They found that soldier presence inhibits pre-soldier differentiation by decreasing the JH level, which is of primary importance in soldier development. JH is released by the corpora allata of insects. Different castes have been found to have different JH levels: levels are low, high, and intermediate in workers, apterous neotenic reproductives, and pre-soldiers, respectively (Chan et al. 2011). Isolated workers that develop into soldiers or neotenic reproductives show different levels of JH synthesis depending on the species (Leniaud et al. 2011). Workers that become pre-soldiers have higher levels of JH synthesis than workers that develop into neotenics. This pattern suggests that, in order to become a soldier, an individual must have high JH levels during its worker and pre-soldier stages (Elliot and Stay 2008). Interestingly, one study shows that JH can have an effect on cuticular hydrocarbon signatures. The hydrocarbon signatures of workers fed filter paper to which a JH analog had been applied were different than those of control workers. Additional differences were found to exist between pre-soldiers and soldiers; furthermore, as soldiers matured, their signatures changed dramatically (Darrouzet et al. 2014). In contrast, JH did not appear to affect cuticular structural constituents in *R. flavipes* (Sen et al. 2013). Mao and Henderson (2010) showed that group size had an effect on both worker JH titers and soldier differentiation in *C. formosanus*: groups of five workers failed to induce soldier differentiation. When soldiers were present, the differentiation of workers into soldiers was less effective; as the number of soldiers present increased, less differentiation occurred. The levels of JH and pheromones are proportional to the ratio of workers to soldiers and thus certainly play a role in upregulating and downregulating the production of the respective castes; furthermore, caste production may also be controlled at the level of the whole colony. However, these various findings may not actually be contradictory because hormone levels and regulatory steps may differ. In these two genera (i.e. *Coptotermes* and *Reticulitermes*), the defensive secretions of soldiers, such as α-pinene and limonene, have not been shown to be antiseptic, as they are in *Nasutitermes* termites (Rosengaus et al. 2000), even though those compounds are produced by soldiers of some *R. flavipes* populations (Quintana et al. 2003). As was mentioned in the introduction, social interactions within *R. flavipes* colonies play a major role in the defense against pathogens, and pathogen defense is a more complex mechanism than previously thought (Chouvenc et al. 2009); this fact is particularly well illustrated by the presence of actinobacteria in the walls of the subterranean nests of *Coptotermes* (Chouvenc et al. 2013).

Caste Social Regulation

As previously discussed, *caste regulation* involves chemical communication and physical contact between nestmates. Even if *Coptotermes* and *Reticulitermes* are the best described termite genera in the literature, most likely because they are urban pests and thus of great economic importance, we still know very little about the genetic or environmental factors acting on their undifferentiated larvae (i.e., their very first larval instars). In these genera, some undifferentiated larvae develop into nymphs (immature instars with wing pads), and nymphs can become alates or brachypterous (nymphoid) neotenics. Undifferentiated larvae may also follow the apterous line of development (the most common fate), in which workers become true workers, soldiers, or apterous (ergatoid) neotenics. This developmental flexibility, first observed by Buchli in 1958 in *Reticulitermes* (and reviewed by Lainé and Wright in 2003), has also been seen in *Coptotermes* species. Since Buchli's work, observations of caste differentiation have mainly taken place in laboratories, sometimes over the course of long-term experiments (Long et al. 2003). Scharf et al. (2003) confirmed the polyphenism that Buchli had observed as well as the caste differentiation and developmental processes that Buchli had described earlier. In addition, they also identified several differentially expressed genes involved in these processes in the main *Reticulitermes* species found in North America: *R. flavipes*. Hayashi et al. (2007) found evidence in *R. speratus,* the Japanese termite, for genetic control of the early developmental bifurcation described above. This flexibility was previously thought to be exclusively regulated by environmental factors, and the epigenetic hypothesis was also well supported. These same authors have observed parthenogenic reproduction in *R. speratus* neotenics (Hayashi et al. 2003; Matsuura et al. 2009a; Matsuura 2011). Parthenogenic reproduction has also been described in other species, such as *R. virginicus* (Vargo et al. 2012), which is endemic to USA, and *R. lucifugus*, which is found in Italy (Luchetti et al. 2013b; see also the following part on Reproduction). This reproductive peculiarity helped reveal that caste determination is the result of a single locus in *R. speratus* (Hayashi et al. 2007). The locus, which is called *dubbed worker*, is X-linked and has two alleles, A and B. They have opposite effects in each sex, but B is always dominant. AA females have the nymph phenotype, as do males with one copy of B. The BB genotype is lethal for females. All other genotypes result in the worker phenotype. However, *R. speratus*' situation may not be reflective of those of all *Reticulitermes* species, and especially not those of species with a slightly biased or unbiased sex ratio, such as the species found in Europe (Lo et al. 2009).

Colonies of *Coptotermes* and *Reticulitermes* that are found in nature in any part of the world can contain several hundreds of thousands of individuals (Forschler and Townsend 1996; Tsunoda et al. 1999); those individuals may forage several dozen or even hundreds of meters away from the nest (Tsunoda et al. 1999; Dronnet et al. 2005). Colonies, particularly those of invasive populations of *Reticulitermes*, may extend across several hectares (Leniaud et al. 2009). This is the reason why colony observation *in natura* is quite impossible. However, genetic tools, such as microsatellite markers that follow Mendelian inheritance, are useful when studying the family structure of colonies, and they can help estimate the number and type of reproductives via F-Statistics and genetics relatedness comparisons (Thorne et al. 1999; Bulmer et al. 2001), and other methods (Vargo and Husseneder 2011). Termite markers were first developed in two intermediate termites (Vargo 2000; Vargo and Henderson 2000; for a review, see Vargo and Husseneder 2009, 2011).

The division of labor between reproductives and workers was probably achieved through minor evolutionary changes; it may be regulated by single genes, such as the *neofem2* gene in the basal termite genus *Cryptotermes* (Weil et al. 2009b; Korb et al. 2009). Although reproduction is genetically or epigenetically controlled, pheromonal cues nonetheless must have an influence. For example, the trade-off between the production of alates and neotenics is mediated by pheromones that act on nymphs or eggs.

Recent research on *R. flavipes* has shown that the presence of soldiers and neotenic reproductives affects the gene expression profile of worker gut symbionts (Sen et al. 2013). Termite gut symbionts may indeed play a role in the regulation of hormones and semiochemicals (such as pheromones) (Wheeler et al. 2010). It has even been speculated that the intestinal bacteria of *R. speratus* may be involved in nestmate recognition (Matsuura 2001). However, the symbiotic community (microbiome), which includes flagellates and bacteria, is poorly described when it comes to its involvement in behavior and caste regulation in intermediate termites (Hu et al. 2011; Boucias et al. 2013; Dedeine et al. in prep). Since stomodeal trophallaxis is relatively common in *Reticulitermes* (Korb et al. 2012), it may play a regulatory role in the transfer of symbiotic fauna.

Sex Recognition, Reproduction, and Fertility Signals

Research examining the *reproductive castes*, neotenics, and winged imagoes (alates) has suggested that chemical communication plays a key role in reproduction. Clément (1982b) and Clément et al. (1989) were the first to describe pheromone attraction in *Reticulitermes* alates. Subsequently, Raina et al. (2003) showed that *C. formosanus* uses a contact sex pheromone: males with ablated antennae failed to demonstrate tandem contact behavior. However, *C. formosanus* does not appear to perform calling behavior as some *Reticulitermes* species do; furthermore, sex pheromones appear to operate in *Reticulitermes* at both short and long distances (Clément 1982b). However, it is interesting to note that the same *Reticulitermes* species, *R. flavipes*, has been found to release different chemical compounds in its populations in France (Laduguie et al. 1994) and in the USA (Clément et al. 1989). Although the compounds are supposedly released by the same gland (the sternal gland located on sternite 5), this assertion is problematic (Bordereau and Pastels 2011); however, different compounds could come into play at different distances and be released by the same or different glands. According to electrophysiological recordings conducted in *C. formosanus*, males respond best to female abdominal tip extracts (Raina et al. 2003); abdominal semiochemicals are assumed to be released by the tergal gland. Antennae play an essential function in communication, especially at the colony foundation stage. Antennal cropping has been observed in paired termites, and it may be used to impair the reception of olfactory signals coming from other potential sexual partners; this behavior could therefore play a role in the pair's transition from group to partnered life (Nalepa et al. 2011). Cues could also potentially be perceived via gustatory organs (the maxillary and labial palps), but this type of perception likely plays a secondary role (Raina et al. 2003). The functions of volatile and contact sex pheromones are still not well described, and the literature is not clear on how the different compounds released by the different glands (sternal, tergal, epidermal, or others yet undescribed) influence behavior. It is possible that the sternal gland produces more volatile compounds, such as the short-chain alcohols (dodecatrienol) used during calling behavior, and that the tergal gland, which is only present in the reproductive caste, produces contact compounds used during tandem behavior; these latter compounds may be lipidic, as in the case of trilinolein or glycerol trilinoleate (Bland et al. 2004). The level of complexity of the different stages of reproductive behavior (pre-swarming involving calling behavior, flight, post-swarming involving tandem running, and mating) varies across species and genera. Dealation (i.e., loss of wings in alates) can provoke a change in the production or composition of chemical compounds, in terms of quality or quantity. The releaser pheromones used by the three genera of intermediate termites (and especially *Coptotermes* and *Heterotermes)* have yet to be clearly identified, even if Batista-Pereira et al. (2004b) have shown that *Heterotermes tenuis* demonstrates somewhat of an electroantennographic response to synthetic dodecatrienol; their effects on behavior and their glands of origin also remain poorly characterized. The role that contact compounds such as long-chain hydrocarbons may play as fertility cues and signals of reproductive status was examined only in lower termites (Liebig et al. 2009); they have been shown to have these functions in other social insects, and it has been suggested that termites might have put to social use the compounds that their cockroach-like ancestors used for sexual communication (Weil et al. 2009b). Nevertheless, reproductive isolation is undoubtedly reinforced by species-specific recognition factors (see the paragraph below on cuticular compounds).

The inhibition of nestmate fertility by reproductives was described in the honeybee many years ago. However, this phenomenon has long been the subject of speculation in termites, and many authors have suggested that a primer pheromone exists in this group. An inhibitory pheromone used by *R. speratus* queens was recently described by Matsuura et al. (2010): it is a volatile pheromone that suppresses the differentiation of new nymphoid queens, but not kings, when a functional queen and other castes are present together. When a functional queen is accompanied by only workers, some workers differentiate into male ergatoid (apterous) neotenics and a few others become female ergatoids. The pheromone, which is only described in secondary queens, was found to be a mixture of *n*-butyl-*n*-butyrate (an ester) and 2-methyl-1-butanol (an alcohol). The same pheromone blend was found on their eggs and serves to attract the workers. The queen pheromone also regulates egg production (Yamamoto and Matsuura 2011). The alcohol lacks chiral specificity, and both its enantiomers ((*R*) and (*S*)), either isolated or present in a racemic mixture, have an inhibitory effect when they co-occur with the ester (Yamamoto et al. 2012). This pheromone is highly volatile and can be described as an honest signal: it disappears when the queen stops laying eggs and it is not transmitted by workers (Matsuura and Yamamoto 2011). The eggs may not only carry this fertility signal but could also potentially synthetize it, as they do synthesize lysozyme, a protein that acts as an antibacterial agent and egg recognition signal (Matsuura et al. 2009b); however, the possible de novo synthesis of this signal remains to be confirmed. Clearly, these volatile pheromones have a multifaceted role: they act as a fertility signal, attract workers, mediate queen-to-queen communication, and serve as antibacterial agents. As a result, they help maintain both reproductive harmony and hygiene in *R. speratus* colonies (Matsuura 2012). As discussed by Blum in various reviews, this type of evolutionary chemical parsimony is commonly seen in the chemical ecology of insects; the same compound, or mixture of compounds, often has various functions in different contexts. Cuticular compounds clearly illustrate this idea, as shall be seen later.

Agonistic behavior, or direct aggressive physical contact among reproductives and/or between reproductives and other castes, is an important part of the control exerted on reproductives. Ghesini and Marini (2009) observed caste differentiation and colony growth in different laboratory colonies of the newly described species *R. urbis* (Bagnères et al. 2003; Uva et al. 2004b). Ghesini and Marini (2009) also showed that nymphs are not able to found viable colonies on their own; they need workers. In colonies containing workers, newly emerged reproductives were eliminated by workers, who allowed only one pair to develop. More importantly, in several experimental colonies, workers eliminated all neotenics that developed from nymphs (nymphoid or brachyperous) but not those that developed from other workers (ergatoid or apterous). This finding is the inverse of what was found in *R. speratus* (Miyata et al. 2004). Nevertheless, workers are perfectly able to differentiate between the different types of secondary reproductives and behave so as to enhance their own indirect fitness, as has been seen in *Pterotermes* (Zimmermann 1983). It is assumed that most neotenics develop from nymphs in *Reticulitermes* species found in nature; however, apterous neotenics may occur when a colony (or part thereof) is left with only a few workers after a natural accident (e.g., a flood or fire), a predator attack, or displacement by humans (Pichon et al. 2007; Leniaud et al. 2011).

Certain conclusions may be drawn from the current state of knowledge on termite fertility signals that have relevance for the directions future research may take. First, the putative fertility signals are species-specific in their chemistry because different queen- and king-specific volatiles have been identified in various species (Himuro et al. 2011) and they differ from the *R. speratus* pheromone. Second, royal pheromones may be much more volatile than assumed in traditional models, which hypothesized that direct physical contact between reproductives and receivers was necessary (Matsuura 2012). Third, it is likely that royal pheromones consist of multiple components (Matsuura et al. 2010; Matsuura 2012). Fourth, in addition to nonpolar hydrocarbons, many other classes of more polar and more volatile compounds, such as alcohols, esters, and acids, should be considered as candidate compounds (Matsuura et al. 2010; Himuro et al. 2011). Fifth, at the same time, non-volatile and non-polar compounds, including CHCs, should not be ruled out, because several levels of signaling are likely. For instance, signals may include the following: (a) long-range inhibitory signals (primer function); (b) fertility-related recognition cues linked with the onset of feeding, tending behavior, or eventual agonism towards superfluous reproductives (releaser function); and (c) sex-specific recognition cues that elicit mating behavior on the part of reproductives of the opposite sex (releaser function). In both (b) and (c), immediate contact recognition of the reproductives is likely and it may be based, for instance, on non-volatile compounds found on the cuticular surface (Matsuura 2012). Sixth, the putative signals should be studied in parallel with possible proteinaceous mediators, carriers, or binding compounds, which may be responsible for the transport, binding, or release of the signal molecules (Hanus et al. 2010; Korb et al. 2009). Seventh, a deeper understanding of these chemical regulation processes requires the identification of the source of the relevant compounds in reproductives. Finally, the chemical profiles of eggs should be studied because egg-produced signals may efficiently convey queen presence and actual fecundity (Bussell and Vosshall 2010; Yamamoto and Matsuura 2011; Matsuura 2012).

Brood Care Behavior

In a subterranean nest, brood (undifferentiated larvae and eggs) are generally clustered in a few nodes of the dispersed polydomous network (Long and Thorne 2006). They may elicit *brood care behavior* by generating odors that accumulate in the nodes. Brood care has recently been shown to comprise several interactive behaviors in various termites from different taxonomic groups, such as *Cryptotermes* (Kalotermitidae), *Zootermopsis* (Termopsidae), *Prorhinotermes* (one-piece-type Rhinotermitidae), and *Reticulitermes* (separate-type Rhinotermitidae) (Korb et al. 2012). A greater degree of egg care and communicative behavior was observed in the most advanced Rhinotermitidae, such as *Reticulitermes* (see Fig. 11.1).

Egg protection and care are among the basic behavioral activities observed in insect societies. Termites are not an exception in this respect; the eggs laid by the queen(s) are collected, handled, piled at specific spots by workers (and in exceptional cases by soldiers; Hanus et al. 2005), and protected from pathogens and desiccation by worker saliva. The recognition of eggs by termite workers has been studied in detail in *Reticulitermes* (Matsuura 2005, 2006; Matsuura and Kobayashi 2007; Matsuura et al. 2007, 2009b). Eggs are recognized by workers on the basis of their shape and surface structure, as well as by chemical cues (Matsuura 2006): the antibacterial protein lysozyme combined with the cellulose-digesting enzyme β-glucosidase, which is produced by the eggs themselves and the salivary glands of tending workers (Matsuura et al. 2007, 2009b). Thus, termites use proteins to mark their eggs. Consequently, the specificity of termite egg recognition is somewhat limited with regards to egg origin, and thus eggs from different colonies and even congeneric species are accepted (Matsuura et al. 2007).

Because of the strong attractive power of these egg pheromonal signals, Matsuura's group has submitted a patent for a termite egg mimic, which could potentially be used in pest control. In different *Reticulitermes* species found in Japan, the USA, and Europe (and studied by the Matsuura and Bagnères groups), cuckoo fungi have been observed to mimic termite eggs, forming what are called termite balls (Yashiro and Matsuura 2007). When they occur in *R. speratus*, the fungi produce lysozyme and β-glucosidase (Matsuura et al. 2009b), which are also found on real eggs, as mentioned above; however, fungal growth can also be inhibited by the two volatile pheromones *n*-butyl-*n*-butyrate and 2-methyl-1-butanol. The proteinaceous compounds are only detected upon contact, while the volatiles act as attractants (Matsuura 2012; Matsuura et al. 2009b).

Altogether, these findings show that brood care behavior has played an important role in termite social evolution. However, apart from the pheromones described by Matsuura et al. (2010) in *R. speratus*, no other egg-produced pheromones have been found in intermediate termite species. Furthermore, no work has yet been done on odor differences between trophic and fertile eggs, a possible area of interest.

The Multifaceted Roles of Cuticular Hydrocarbons in Recognition

Cuticular hydrocarbons are mixtures of several dozen long-chain hydrocarbons that typically contain 20–40 carbon atoms; these hydrocarbons can be branched (methylated), unsaturated (alkenes such as monoenes and dienes), or saturated (linear alkanes) (Blomquist and Bagnères 2010). Their role is known to be multifaceted (LeConte and Hefetz 2008).

Batista-Pereira et al. (2004a) performed the only electrophysiological study to date on termite CHCs; they used a total hexane extract from workers of *Heterotermes tenuis*. When *H. tenuis* antennae came in contact with pieces of paper impregnated with varying concentrations of the extract, an electroantennographic response was provoked that, depending on the extract concentration, was usually significantly higher than the mean response to the controls. The extracts mostly contained methyl-branched hydrocarbons. The results of this preliminary experiment were supported by behavioral bioessays performed using cuticular extracts in a Y-tube choice experiment. This experiment was, curiously, never repeated using other termite taxa. Direct evidence were also obtained in experiments in which a non-nestmate CHC blend was topically applied to termites; said termites were then perceived as aliens by their congeners (Howard et al. 1982a; Bagnères et al. 1991; Takahashi and Gassa 1995). In termites, hydrocarbons are secreted by oenocytes and transported to and from the cuticular surface by lipophorins (Sevala et al. 2000; Fan et al. 2004). Lipophorin titers differed among castes and were highest in nymphs; among workers, older termites had the highest levels (Fan et al. 2004). It was shown some time ago that there is variation in cuticular hydrocarbons among castes in *Reticulitermes* and *Coptotermes* (Howard et al. 1982a; Haverty et al. 1996; Bagnères et al. 1998).

In the 1998 paper, Bagnères and colleagues suggested that caste recognition within a colony is a sensory process during which nestmates pick up on minute variations in CHC mixtures. This process was modeled using a mathematical approach that employed artificial neural networks (ANNs) (Bagnères et al.1998). In the various *Reticulitermes* species studied, network performance allowed termites to discriminate among the chemical patterns of the different castes. It was assumed that this sensory process, starting with CHC perception (mediated by the antennae) and ending with recognition behavior, relies on minute variations in the relative proportions of hydrocarbons among castes. Due to the mutual transmission of CHCs, the caste specificity of CHC signatures can influence general colony odor and reflect the actual caste composition of a colony. For instance, having a high proportion of nymphs in a colony can shift the colony's CHC profile, which can thus serve as a cue for the presence of nymphs and influence the acceptance or rejection of non-nestmates (Uva et al. 2004a). The different castes of *R. flavipes* appear to be well differentiated in terms of their relative proportions of different hydrocarbons (soldiers, younger vs. older larval stages, and neotenics) (Darrouzet et al. 2014). In this termite species (and in other European species), caste-specific signatures are stronger than colony-specific signatures (Bagnères personal observation).

A number of studies examining the importance of CHCs in nestmate and sexual recognition have been conducted on *Reticulitermes* and *Heterotermes* termites, as CHCs have been shown to play a role in these processes in other termites (Kaib et al. 2002, 2004; Weil et al. 2009b; see also the related paragraphs). Shorter but not to be ignored is the list of studies showing no correlation between CHC patterns and aggression (e.g., Su and Haverty 1991). Cuticular mixtures form colonial signatures that are perceived via grooming using the whole antenna; if the perceived signature differs from the colony's chemotype, agonistic behavior may result (Clément 1981, 1982a; Bagnères 1989; Clément and Bagnères 1998; Haverty et al. 1999; Batista-Pereira et al. 2004a; Costa-Leonardo and Haifig 2010; Huang et al. 2012a). It has also been found that, within a given colony, some individual termites are systematically more aggressive than others (Polizzi and

Forschler 1999). Colony signatures are also constantly changing (Bagnères et al. 2011). The CHC bouquet that constitutes the specific odor of a colony is genetically determined and thus heritable; however, epigenetic and environmental factors seem to contribute to colony odor as well (Adams 1991; Husseneder et al. 1997, 1998; Kaib et al. 2002; Dronnet et al. 2006). Individual chemical signatures are homogenized among nestmates by frequent mutual contacts and grooming, as evidenced by the fact that the artificial mixing of colonies results in a mixed CHC pattern (Vauchot et al. 1996, 1998). Not all the components of the CHC signature necessarily contribute to recognition. Just as in other social insects (van Zweden and d'Ettorre 2010; Constanzi et al. 2013), branched and/or unsaturated hydrocarbons are thought to play the greatest role in conveying information, while linear alkanes appear to primarily serve to protect against desiccation, the primary function of CHCs. In social insects, the cognition process that underlies the perception of CHCs as recognition cues seems to function by constantly comparing the chemical profiles of the individuals being assessed with a template of colony odor; it is thought that termites detect the presence of foreign elements rather than shared elements. Thus, recognition is less about recognizing nestmates than recognizing non-nestmates with dissimilar chemical profiles (Guerrieri et al. 2009). The template for colony odor (Gestalt odor) seems to be generated by averaging the chemical profiles of nestmates; this template may simply be the consequence of habituation to frequently encountered odors rather than a long-term memory (see van Zweden and d'Ettorre 2010). However, some results suggest that termites can remember their colony's odor for at least several months (Olugbemi 2013). The acceptance threshold would therefore be a combination of, on the one hand, the readiness of acceptance demonstrated by the termite performing the assessment and, on the other hand, nestmate CHC diversity, which is determined by genetic diversity and environmental factors. This model can be applied across closed and open societies. In societies with numerous unrelated reproductives, offspring will be more genetically and chemically diversified, thus the template will be richer and the acceptance threshold lower (e.g., Takematsu and Kambara 2012). The inverse should also be true; emerging populations with low genetic diversity may demonstrate openness because the heritable elements of CHC patterns also show limited diversity throughout the entire population (e.g., Dronnet et al. 2006; Perdereau et al. 2010a, b, 2011).

Environmental factors can modify heritable CHC signatures. Clinal variability and temperature are known to affect CHC patterns in termites and may thus be the epigenetic causes of the CHC profile divergences (Woodrow et al. 2000; Uva et al. 2004a) that are revealed by termite population structure (Vargo et al. 2013). It has been suggested that the composition of the intestinal symbiotic fauna has a dramatic effect on intercolonial agonism and thus acts as a recognition cue in *Reticulitermes speratus* (Matsuura 2001), *C. formosanus* (Wei et al. 2007), and *H. mossambicus* (Kirchner and Minkley 2003; Minkley et al. 2006). This hypothesis is compatible with the CHC paradigm, given that intestinal microorganisms presumably supply the termite host with hydrocarbon precursors (Guo et al. 1991). A strong correlation between diet and aggression has been reported in a few cases, which suggests that diet-derived chemicals directly contribute to the recognition process (e.g., Florane et al. 2004) or that the availability of CHC precursors may shift depending on termite diet (Rojas et al. 2005).

The importance of CHCs in termite recognition is clearly underscored by their role in species recognition. CHCs are an excellent chemotaxonomic tool because they are species-specific (Brown et al. 1990; Clément et al. 2001; Howard and Blomquist 2005; review in Bagnères and Wicker-Thomas 2010). Termites can live in natural or artificial heterospecific colonies by employing chemical mimicry or by modulating their species-specific CHC signatures. This observation shows that CHC signatures are an important part of the social life style. This point is further illustrated by cases in which natural or experimental cheating results in non-relatives or parasites being integrated into foreign colonies (Howard et al. 1980, 1982b; Vauchot et al. 1996, 1998), which also occurs in other social insects (Bagnères and Lorenzi 2010). Using de novo synthesis or passive transfer, termites can change the proportion or even the type of cuticular compounds that make up their specific chemical signature, an ability that is key to colony life.

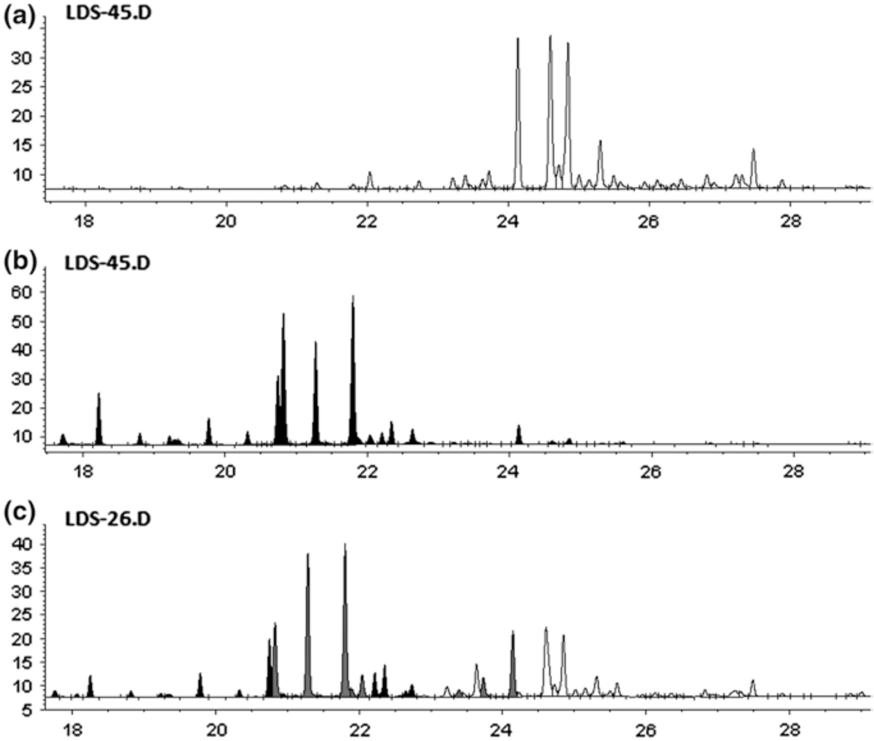


Fig. 11.4 Chemical signatures from: **a** *Reticulitermes* larvae from a *R. grassei* homospecific couple; **b** *Reticulitermes* larvae from a *R. flavipes* homospecific couple; **c** Hybrid larvae from a heterospecific couple (♂Rg♀Rf) isolated from their parents. From De Schreyer (2011) (typical Rg peaks are in white; typical Rf peaks are in black)

An experiment by the Bagnères team (De Schreyer 2011) showed that when alates from two different *Reticulitermes* species mated, their brood had a hybrid signature (Fig. 11.4). This finding strongly supports the idea that chemical signatures are genetically transmitted by both parents.

The similarity between the cuticular signatures of *R. santonensis*, found in France, and *R. flavipes*, found in the USA (Bagnères et al. 1990a), provided the first indication that an invasion had taken place. Indeed, it was later shown that *R. santonensis* had been misidentified; the "species" turned out to be *R. flavipes*, which had become established in France (and other parts of the world) after several of its founders had arrived from Louisiana, most likely when it was still a French colony (Perdereau et al. 2010b, 2011, 2013). The CHC data confirm the DNA data. They also show that the cuticular signature of the *R. flavipes* population found in France is strongly chemically homogenous, which may explain the lack of agonistic behavior among colonies; a similar pattern has been observed in other invasive species, such as the Argentine ant (Vasquez et al. 2009). Temperate subterranean termites belonging to *Reticulitermes*, *Coptotermes*, and *Heterotermes* live in a wide variety of ecosystems. They are also among the most invasive urban pests in the world. While their flexible reproductive development certainly contributes to their success as invaders, it may be that the flexibility of their chemical communication systems also plays a role.

Conclusions

It is surprising to see how few termite species have been studied in detail with respect to basic aspects of their biology, including communication. One can literally count the number of species with the fingers of two hands. However, the number of papers on termites that have come out over the last decade is promising, and we can hope that the work published thus far will encourage research on lesser known species in the future. Indeed, "omics" are now commonly used to explore the interplay between biology, physiology, genetics, and behavior. For example, several studies underscore the potential of molecular techniques when it comes to increasing our understanding of communication and social regulation in insects in general and termites in particular; these studies include analyses of the head tissue transcriptome and genes expressed during caste differentiation and aggression (Huang et al. 2012b), pheromone-mediated gene expression (Grozinger et al. 2003), trail-following behavior (Schinghammmer et al. 2011), and RNAi-mediated gene silencing (Zhu et al. 2013). This latter study supports the idea that some receptors show compound specificity in relation to specific behaviors. Molecular tools should also be used to take a new look at less recent research on termite evolution. Recent high-quality work by Kobayashi et al. (2013) relied on an impressive collection of termite colonies obtained in the field, and their results have contributed significantly to the ongoing discussion on inclusive fitness theory in non-hymenopteran insects. Indeed, more experimental studies should be performed in the field rather than in laboratories, which is not contradictory to more omic studies. At present, it is still very difficult to appreciate how a colony, particularly a colony of subterranean termites, really lives *in natura*. For example, although we can calculate the theoretic reproductive potential of termite societies thanks to molecular tools, such as the polymorphic markers first developed for termites by Vargo and colleagues, we cannot estimate their actual reproductive potential. We are now in a post-genomic world when it comes to chemical communication (Berenbaum and Robinson 2003). For instance, numerous research teams currently use complex, chemistry-based analytical tools to conduct chemical ecology studies, and there is shared interest in using "omics" techniques (such as metabolomics, proteomics, genomics, phylogenomics, etc.) to study more and more complex organisms and communities of organisms. In social insects in general, more research should be devoted to studying the ancestral role of cuticular hydrocarbons (Van Oystaeyen et al. 2014), as well as their current multifarious roles; in particular, their function in regulatory processes should be examined. Because of the exceptional complexity of termite caste and reproductive systems, termites will undoubtedly become better characterized model organisms thanks to this fresh, multidisciplinary perspective.

Acknowledgments The authors wish to thank Jessica Pearce for English revision and Ed Vargo for precious comments on the manuscript. RH acknowledges the support by the Academy of Sciences of the Czech Republic (RVO 61388963).

References

Abe T (1987) Evolution of life types in termites. In: Kawanno S, Connell JH, Hidaka T (eds) Evolution and coadaptation in biotic communities. University of Tokyo Press, Tokyo, pp 125–148

Abe T (1990) Evolution of worker caste in termites. In: Veeresh GK, Mallik B, Viraktamath CA (eds) Social insects and the environment. Proceedings 11th international congress IUSSI 1990, Bangalore, India. Oxford & IBH, New Delhi, pp 29–30

Adams ES (1991) Nest-mate recognition based on heritable odors in the termite *Microcerotermes arboreus*. Proc Natl Acad Sci USA 88:2031–2034

Adams ES, Atkinson L, Bulmer MS (2007) Relatedness, recognition errors, and colony fusion in the termite *Nasutitermes corniger*. Behav Ecol Sociobiol 61:1195–1201

Affolter J, Leuthold RH (2000) Quantitative and qualitative aspects of trail pheromones in *Macrotermes subhyalinus* (Isoptera, Termitidae). Insect Soc 47:256–262

Atkinson L, Teschendorf G, Adams ES (2008) Lack of evidence for nepotism by workers tending queens of the polygynous termite *Nasutitermes corniger*. Behav Ecol Sociobiol 62:805–812

Badertscher S, Gerber C, Leuthold RH (1983) Polyethism in food supply and processing in termite colonies of *Macrotermes subhyalinus* (Isoptera). Behav Ecol Sociobiol 12:115–119

Bagine RKN, Brandl R, Kaib M (1990) Cuticular hydrocarbon profiles as a systematical tool: a case study in the termite genus *Odontotermes*. In: Veeresh GK, Mallik B, Viraktamath CA (eds) Social insects and the environment. Proceedings 11th international congress IUSSI 1990, Bangalore, India. Oxford & IBH, New Delhi, p 28

Bagine RKN, Brandl R, Kaib M (1994) Species delimitation in *Macrotermes* (Isoptera: Macrotermitinae): evidence from epicuticular hydrocarbons, morphology, and ecology. Ann Entomol Soc Am 87:498–506

Bagnères A-G (1989) Les hydrocarbures cuticulaires des insectes sociaux: Détermination et rôle dans la reconnaissance spécifique, coloniale et individuelle. Ph.D. thesis, Université Pierre et Marie Curie, Paris

Bagnères A-G, Lorenzi C (2010) Chemical deception/mimicry using cuticular hydrocarbons. In: Blomquist GJ, Bagnères A-G (eds) Insect hydrocarbons: biology, biochemistry and chemical ecology. Cambridge University Press, Cambridge, pp 282–324

Bagnères A-G, Wicker-Thomas C (2010) Chemical taxonomy with hydrocarbons. In: Blomquist GJ, Bagnères A-G (eds) Insect hydrocarbons: biology, biochemistry, and chemical ecology. Cambridge University Press, Cambridge, pp 121–162

Bagnères A-G, Clément J-L, Blum MS et al (1990a) Cuticular hydrocarbons and defensive compounds of *Reticulitermes flavipes* (Kollar) and *R. santonensis* (Feytaud): polymorphism and chemotaxonomy. J Chem Ecol 16:3213–3244

Bagnères A-G, Clément J-L, Lange C, Blum MS (1990b) Cuticular compounds in *Reticulitermes* termites: species, caste and colonial signature. In: Veeresh GK, Mallik B, Viraktamath CA (eds) Social insects and the environment. Proceedings 11th international congress IUSSI 1990, Bangalore, India. Oxford & IBH, New Delhi, pp 423–424

Bagnères A-G, Killian A, Clément J-L, Lange C (1991) Interspecific recognition among termites genus *Reticulitermes*: evidence for a role for the cuticular hydrocarbons. J Chem Ecol 17:2397–2420

Bagnères A-G, Rivière G, Clément J-L (1998) Artificial neural network modeling of caste odor discrimination based on cuticular hydrocarbons in termites. Chemoecology 8:201–209

Bagnères A-G, Uva P, Clément J-L (2003) Description d'une nouvelle espèce de termite: *Reticulitermes urbis* n. sp. (Isopt., Rhinotermitidae). Bull Soc Entomol Fr 108:433–435

Bagnères A-G, Darrouzet E, Landré X, Christidès JP (2011) Endogenous synchronization of the chemical signature of *Reticulitermes* (Isoptera, Rhinotermitidae) worker termites. Ann Soc Entomol Fr 47:202–208

Batista-Pereira LG, dos Santos MG, Correa AG et al (2004a) Cuticular hydrocarbons of *Heterotermes tenuis* (Isoptera: Rhinotermitidae): analyses and electrophysiological studies. Z Naturforsch 59:135–139

Batista-Pereira LG, dos Santos MG, Corrêa AG et al (2004b) Electroantennographic responses of *Heterotermes tenuis* (Isoptera: Rhinotermitidae) to synthetic (3*Z*,6*Z*,8*E*)-dodecatrien-1-ol. J Braz Chem Soc 15:372–377

Berenbaum MR, Robinson GE (2003) Chemical communication in a post-genomic world. Proc Natl Acad Sci USA 100:14513

Bignell DE, Eggleton P (2000) Termites in ecosystems. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Press, Dordrecht, pp 363–387

Bland JM, Park YI, Raina AK et al (2004) Trilinolein identified as a sex specific component of tergal glands in alates of *Coptotermes formosanus*. J Chem Ecol 30:835–849

Blomquist GJ, Bagnères A-G (2010) Insect hydrocarbons, biology, biochemistry, and chemical ecology. Cambridge University Press, Cambridge

Blomquist GJ, Howard RW, McDaniel CA (1979) Structures of the cuticular hydrocarbons of the termite *Zootermopsis angusticollis* (Hagen). Insect Biochemistry 9:365–370

Blomquist GJ, Tillman JA, Mpuru S, Seybold SJ (1998) The cuticle and cuticular hydrocarbons of insects: structure, function, and biochemistry. In: Van der Meer RK, Breed MD, Espelie KE, Winston ML (eds) Pheromone communication in social insects: ants, wasps, bees and termites. Westview Press, Boulder, pp 34–54

Blum MS (1987) Specificity of pheromonal signals: a search for its recognitive bases in terms of a unified chemisociality. In: Eder J, Rembold H (eds) Chemistry and biology of social insects. Verlag Perperny, Munich, pp 401–405

Bonabeau E, Theraulaz G, Deneubourg JL et al (1997) Self-organization in social insects. Trends Ecol Evol 12:188–193

Bonabeau E, Theraulaz G, Deneubourg JL et al (1998) A model for the emergence of pillars, walls and royal chambers in termite nests. Phil Trans R Soc Lond B Biol Sci 353:1561–1576

Bonavita-Courgourdan A, Clément J-L, Lange C (1987) Nestmate recognition: the role of cuticular hydrocarbons in the ant *Camponotus vagus* Scop. J Entomol Sci 22:1–10

Bonckaert W, Drijfhout FP, d'Ettore P et al (2012) Hydrocarbon signature of egg maternity, caste membership and reproductive status in the common wasp. J Chem Ecol 38:42–51

Bordereau C (1985) The role of pheromones in termite caste differentiation. Curr Themes Trop Sci 3:221–226

Bordereau C, Han SH (1986) Stimulatory influence of the queen and king on soldier differentiation in the higher termites *Nasutitermes lujae* and *Cubitermes fungifaber*. Insect Soc 33:296–305

Bordereau C, Pasteels JM (2011) Pheromones and chemical ecology of dispersal and foraging in termites. In: Bignell DE, Roisin Y, Lo N (eds) Biology of termites: a modern synthesis. Springer, Dordrecht, pp 279–320

Bordereau C, Robert A, Laduguie N et al (1993) Détection du (Z, Z, E)-3,6,8-dodecatrièn-1-ol par les ouvriers et les essaimants de deux espèces de termites champignonnistes: Pseudacanthotermes spiniger et P. militaris (Termitidae, Macrotermitidae). Act Coll Insectes Soc 8:145–149

Bordereau C, Robert A, Van Tuyen V, Peppuy A (1997) Suicidal defensive behavior by frontal gland dehiscence in *Globitermes sulphureus* Haviland soldiers (Isoptera). Insect Soc 44:289–296

Bordereau C, Cancello EM, Sémon E et al (2002) Sex pheromone identified after solid phase microextraction from tergal glands of female alates in *Cornitermes bequaerti* (Isoptera, Nasutitermitinae). Insect Soc 49:209–215

Bordereau C, Lacey MJ, Sémon E et al (2010) Sex pheromones and trail-following pheromone in the basal termites *Zootermopsis nevadensis* (Hagen) and *Z. angusticollis* (Hagen) (Isoptera: Termopsidae: Termopsinae). Biol J Linnean Soc 100:519–530

Bordereau C, Cancello EM, Sillam-Dussès D, Sémon E (2011) Sex-pairing pheromones and reproductive isolation in three sympatric *Cornitermes* species (Isoptera, Termitidae, Syntermitinae). J Insect Physiol 57:469–474

Bos N, Dreier S, Jørgensen CG et al (2012) Learning and perceptual similarity among cuticular hydrocarbons in ants. J Insect Physiol 58:138–146

Boucias DG, Cai Y, Sun Y et al (2013) The hingut lumen prokaryotic microbiota of the termtie *Reticulitermes flavipes* and its responses to dietery lignocelluloses composition. Mol Ecol 22:1836–1853

Breed MD (1987) Kin recognition in highly eusocial insects. In: Fletcher DJC, Michener CD (eds) Kin recognition in animals. Wiley, Chichester, New York, pp 243–285

Breed MD, Buchwald R (2009) Cue diversity and social recognition. In: Gadau J, Fewell J (eds) Organization of insect societies—from genome to sociocomplexity. Harvard University Press, Cambridge, pp 173–194

Brent CS (2009) Control of termite caste differentiation. In: Gadau J, Fewell J (eds) Organization of insect societies—from genome to sociocomplexity. Harvard University Press, Cambridge, pp 105–127

Brown WV, Watson JAL, Carter FL, Lacey MJ, Barrett RA, McDaniel CA (1990) Preliminary examination of cuticular hydrocarbons of worker termites as chemotaxonomic characters for some Australian species of *Coptotermes* (Isoptera: Rhinotermitidae). Sociobiology 16:305–328

Brown WV, Watson JAL, Lacey MJ (1996a) A chemotaxonomic survey using cuticular hydrocarbons of some species of the Australian harvester termite genus *Drepanotermes* (Isoptera: Termitidae). Sociobiology 27:199–221

Brown WV, Watson JAL, Lacey MJ et al (1996b) Composition of cuticular hydrocarbons in the Australian harvester termite *Drepanotermes perniger* (Isoptera: Termitidae): variation among individuals, castes, colonies and locations. Sociobiology 27:181–197

Bruinsma OM (1979) An analysis of building behaviour of the termite *Macrotermes subhyalinus*. Doctoral thesis, Agricultural University, Wageningen

Buchli HHR (1958) L'origine des castes et les potentialities ontogéniques des termites européens du genre *Reticulitermes* Holmgren. Ann Sci Nat Zool 11:267–429

Bulmer MS, Adams ES, Traniello JFA (2001) Variation in colony structure in the subterranean termite *Reticulitermes flavipes*. Behav Ecol Sociobiol 49:236–243

Bussell JJ, Vosshall LB (2010) Chemical ecology: reprogramming a termite monarchy. Nature Chem Biol 6:637–638

Cancello EM, DeSouza O (2004) A new species of *Glossotermes* (Isoptera): reappraisal of the generic status with transfer from the Rhinotermitidae to the Serritermitidae. Sociobiology 44:1–19

Casarin FA, Arab A, Costa-Leonardo AM (2003) Influence of the labial gland's semiochemicals on the feeding behavior of *Coptotermes havilandi* (Isoptera: Rhinotermitidae). Sociobiology 42:485–493

Castle GB (1934) The damp-wood termites of the western United States, genus *Zootermopsis* (formerly, *Termopsis*). In: Kofoid CA (ed) Termites and termite control. University of California Press, Berkeley, pp 273–310

Châline N, Sandoz JC, Martin SJ et al (2005) Learning and discrimination of individual cuticular hydrocarbons by honeybees (*Apis mellifera*). Chem Senses 30:327–335

Chan KK, Abel DS, Stay B (2011) Fine structure of corpora allata of castes with different rates of juvenile hormone production in the termite *Reticulitermes flavipes*. Arthropod Struct Dev 40:26–38

Chen JA, Henderson G, Grimm CC et al (1998) Termites fumigate their nests with naphtalene. Nature 392:558

Chen JA, Henderson G, Laine RA (1999) Lignoceric acid and hexanoic acid: major components of soldier frontal gland secretions of the Formosan subterranean termite (*Coptotermes formosanus*). J Chem Ecol 25:817–824

Chouvenc T, Su NY, Robert A (2009) Cellular encapsulation in the eastern subterranean termite, *Reticulitermes flavipes* (Isoptera), against infection by the entomopathogenic fungus *Metarhizium anisopliae*. J Invertebr Pathol 101:234–241

Chouvenc T, Efstathion CA, Elliot ML, Su NY (2013) Extended disease resistance emerging from the faecal nest of a subterranean termite. Proc R Soc B 280:20131885

Clément J-L (1981) Recognition behavior in the genus *Reticulitermes* (Isoptera). C R Acad Sci 292:931–933

Clément J-L (1982a) Signaux de contact responsables de l'agression interspécifique des termites du genre *Reticulitermes* (Isoptères). C R Acad Sci 294:635–638

Clément J-L (1982b) Phéromones d'attraction sexuelle des termites européens du genre *Reticulitermes* (Rhinotermidae). Mécanismes comportementaux et isolements spécifiques. Biol Behav 7:55–69

Clément J-L (1986) Open and closed societies in *Reticulitermes* termites (Isoptera, Rhinotermitidae): geographic and seasonal variation. Sociobiology 11:311–323

Clément J-L, Bagnères A-G (1998) Nestmate recognition in termites. In: Van der Meer RK, Breed MD, Espelie KE, Winston ML (eds) Pheromone communication in social insects: ants, wasps, bees and termites. Westview Press, Boulder, pp 126–155

Clément J-L, Lemaire M, Nagnan P et al (1988) Chemical ecology of European termites of the genus *Reticulitermes*: allomones, pheromones and kairomones. Sociobiology 14:165–174

Clément J-L, Lloyd H, Nagnan P, Blum MS (1989) *n*-Tetradecyl propionate: identification as a sex pheromone of the eastern subterranean *Reticulitermes flavipes* (Isoptera, Rhinotermitidae). Sociobiology 31:131–142

Clément J-L, Bagnères A-G, Uva P et al (2001) Biosystematics of *Reticulitermes* termites in Europe: morphological, chemical and molecular data. Insect Soc 48:202–215

Connétable S, Robert A, Bouffault F, Bordereau C (1999) Vibratory alarm signals in two sympatric higher termite species: *Pseudacanthotermes spiniger* and *P. militaris* (Termitidae, Macrotermitinae). J Insect Behav 12:329–342

Connétable S, Robert A, Bordereau C (2012) Dispersal flight and colony development in the fungus-growing termites *Pseudacanthotermes spiniger* and *P. militaris*. Insect Soc 59:269–277

Constanzi E, Bagnères A-G, Lorenzi MC (2013) Changes in the hydrocarbon proportions of colony odor and their consequences on nestmate recognition in social wasps. PLoS ONE 8:e65107

Costa JT (2006) The ecology of social evolution. In: Costa JT (ed) The other insect societies. Belknap Press of Harvard University Press, London, pp 16–45

Costa-Leonardo AM, Haifig I (2010) Pheromones and exocrine glands in Isoptera. In: Litwack G (ed) Pheromones. Vitamins and hormones, vol 83. Elsevier, London, pp 521–546

Costa-Leonardo AM, Haifig I (2014) Termite communication during different behavioral activities. In: Witzani G (ed) Biocommunication of animals. Springer Science+Business Media, Dordrecht. doi:10.1007/978-94-007-7414-8_10

Costa-Leonardo AM, Casarin FE, Lima JT (2009) Chemical communication in Isoptera. Neotrop Entomol 38:1–6

Cvačka J, Jiroš P, Šobotník J et al (2006) Analysis of insect cuticular hydrocarbons using matrix-assisted laser desorption/ionization mass spectrometry. J Chem Ecol 32:409–434

D'Ettore P, Lenoir A (2010) Nestmate recognition. In: Lach L, Parr CL, Abbott KL (eds) Ant ecology. Oxford University Press, Oxford, pp 190–205

Darlington JPEC (1982) The underground passages and storage pits used in foraging by a nest of the termite *Macrotermes michaelseni* in Kajiado, Kenya. J Zool 198:237–247

Darrouzet E, Labédan M, Landré X et al (2014) Endocrine control of cuticular hydrocarbon profiles during worker-to-soldier differentiation in the termite *Reticulitermes flavipes*. J Insect Physiol 61:25–33

De Rhoode JC, Lefèvre T, Hunter MD (2013) Self-medication in animals. Science 340:150–151

De Schreyer L (2011) Analyse de la signature chimique mixte et hybride des individus issus des croisements *Reticulitermes flavipes* et *Reticulitermes grassei*. Rapport de stage 2e année bachelier Chimie Biotechnologie. Institut R. Lambion CERIA Bruxelles/IRBI Tours. 61p.

De Souza DJ, Lenoir A, Kasuya MC et al (2013) Ectosymbionts and immunity in the leaf-cutting ant *Acromyrmex subterraneus subterraneus*. Brain Behav Immun 28:182–187

Dong SL, Mao L, Henderson G (2009) Physical contact between soldier and worker is essential in soldier self-regulation of *Coptotermes formosanus* (Isoptera, Rhinotermitidae). Insect Soc 56:28–34

Dronnet S, Chapuisat M, Vargo EL et al (2005) Genetic analysis of the breeding system of an invasive subterranean termite, *Reticulitermes santonensis,* in urban and natural habitats. Mol Ecol 14:1311–1320

Dronnet S, Lohou C, Christidès J-P, Bagnères A-G (2006) Cuticular hydrocarbon composition reflects genetic relationship among colonies of the introduced termite *Reticulitermes santonensis* Feytaud. J Chem Ecol 32:1027–1042

Dunn R, Messier S (1999) Evidence for the opposite of the dear enemy phenomenon in termites. J Insect Behav 12:461–464

Eggleton P (2011) An introduction to termites: biology, taxonomy and functional morphology. In: Bignell DE, Roisin Y, Lo N (eds) Biology of termites: a modern synthesis. Springer, Dordrecht, pp 1–26

Eisner T, Kriston I, Aneshansley DJ (1976) Defensive behavior of a termite (*Nasutitermes exitiosus*). Behav Ecol Sociobiol 1:83–125

Eliyahu D, Ross KG, Haight KL et al (2011) Venom alkaloid and cuticular hydrocarbon profiles are associated with social organization, queen fertility status and queen genotype in the fire ant *Solenopsis invicta*. J Chem Ecol 37:1242–1254

Elliot KL, Stay B (2008) Changes in juvenile hormone synthesis in the termite *Reticulitermes flavipes* during development of soldiers and neotenic reproductives from groups of isolated workers. J Insect Physiol 54:492–500

Engel MS, Grimaldi DA, Krishna K (2009) Termites (Isoptera): their phylogeny, classification, and rise to ecological dominance. Am Mus Novit 3650:1–27

Evans TA, Lai JCS, Toledano E et al (2005) Termites assess wood size by using vibration signals. Proc Natl Acad Sci USA 102:3732–3737

Evans TA, Inta R, Lai JCS, Lenz M (2007) Foraging vibration signals attract foragers and identify food size in the drywood termite, *Cryptotermes secundus*. Insect Soc 54:374–382

Evans TA, Inta R, Lai JCS et al (2009) Termites eavesdrop to avoid competitors. Proc R Soc B 276:4035–4041

Fan Y, Schal C, Vargo EL, Bagnères A-G (2004) Characterization of termite lipophorin and its involvement in hydrocarbon transport. J Insect Physiol 50:609–620

Florane CB, Bland JM, Husseneder C, Raina AK (2004) Diet-mediated inter-colonial aggression in the Formosan subterranean termite *Coptotermes formosanus*. J Chem Ecol 30:2559–2574

Forschler BT, Townsend ML (1996) Mark-release-recapture estimates of *Reticulitermes* spp. (Isoptera: Rhinotermitidae) colony foraging populations from Georgia, USA. Environ Entomol 25:952–962

Fuller CA (2007) Fungistatic activity of freshly killed termite, *Nasutitermes acajutlae*, soldiers in the Caribbean. J Insect Sci 7:14

Gao Q, Bidochka MJ, Thompson GJ (2012) Effect of group size and caste ratio on individual survivorship and social immunity in a subterranean termite. Acta Ethol 15:55–63

Gerber C, Badertscher S, Leuthold RH (1988) Polyethism in *Macrotermes bellicosus* (Isoptera). Insect Soc 35:226–240

Gessner S, Leuthold RH (2001) Caste-specificity of pheromone trails in the termite *Macrotermes bellicosus*. Insect Soc 48:238–244

Ghesini S, Marini M (2009) Caste differentiation and growth of laboratory colonies of *Reticulitermes urbis* (Isoptera, Rhinotermitidae). Insect Soc 56:309–318

Gonçalves TT, DeSouza O, Billen J (2010) A novel exocrine structure of the bicellular unit type in the thorax of termites. Acta Zool 91:193–198

Grassé PP (1959a) La reconstruction du nid et les coordinations inter-individuelles chez *Bellicositermes natalensis* et *Cubitermes* sp. La theorie de la stigmergie: Essai d'interpretation des termites constructeurs. Insect Soc 6:41–83

Grassé PP (1959b) Nouvelles expériences sur le termite de Müller (*Macrotermes muller*) et considérations sur la théorie de la stigmergie. Insect Soc 14:73–102

Grassé PP (1982) Termitologia. Tome I. Anatomie, Physiologie, Reproduction des termites. Masson, Paris

Grassé PP (1984). Termitologia. Tome II. Fondation des société, Construction. Masson, Paris

Grassé PP (1986). Termitologia. Tome III. Comportement, Socialité, Ecologie, Evolution, Systématique. Masson, Paris

Grassé PP, Noirot C (1946) La production des sexués néoteniques chez le termite à cou jaune (*Calotermes flavicollis* F.): inhibition germinale et inhibition somatique. C R Acad Sci 223:869–871

Grassé PP, Noirot C (1958) La société de *Calotermes flavicollis* (Insecte Isoptère) de sa fondation au premier essaimage. C R Acad Sci 246:1789–1795

Greenberg SLW, Plavcan KA (1986) Morphology and chemistry of the mandibular gland complex in the primitive termite, *Zootermopsis angusticollis* (Hagen) (Isoptera: Hodotermitidae). Int J Insect Morphol Embryol 15:283–292

Greenberg SLW, Stuart AM (1980) Control of neotenic development in a primitive termite (Isoptera: Hodotermitidae). J N Y Entomol Soc 88:49–50

Greenberg SLW, Stuart AM (1982) Precocious reproductive development (neoteny) by larvae of a primitive termite *Zootermopsis angusticollis* (Hagen). Insect Soc 29:535–547

Greene MJ, Gordon DM (2003) Cuticular hydrocarbons inform task decision. Nature 432:32

Grozinger CM, Sharabash NM, Whitfield CW, Robinson GE (2003) Pheromone-mediated gene expression in the honey bee brain. Proc Natl Acad Sci USA 100:14519–14525

Guerrieri FJ, Nehring V, Jorgensen CG et al (2009) Ant recognize foes and not friend. Proc R Soc B 276:2461–2468

Guo L, Quilici DR, Chase J, Blomquist GJ (1991) Gut tract microorganisms supply the precursors for methyl-branched hydrocarbon biosynthesis in the termite, *Zootermopsis nevadensis*. Insect Biochem 21:327–333

Hacker M, Kaib M, Bagine RKN et al (2005) Unrelated queens coexist in colonies of the termite *Macrotermes michaelseni*. Mol Ecol 14:1527–1532

Hanus R, Šobotník J, Cizek L (2005) Egg care by termite soldiers. Insect Soc 52:357–359

Hanus R, Luxová A, Šobotník J et al (2009) Sexual communication in the termite *Prorhinotermes simplex* (Isoptera, Rhinotermitidae) mediated by a pheromone from female tergal glands. Insect Soc 56:111–118

Hanus R, Vrkoslav V, Hrdý I et al (2010) Beyond cuticular hydrocarbons: evidence of proteinaceous secretion specific to termite kings and queens. Proc R Soc B 277:995–1002

Hanus R, Šobotník J, Krasulová J et al (2012) Nonadecadienone, a new termite trail-following pheromone identified in *Glossotermes oculatus* (Serritermitidae). Chem Senses 37:55–63

Hartke TR, Rosengaus RB (2013) Costs of pleometrosis in a polygamous termite. Proc R Soc B 280

Haverty MI (1977) The proportion of soldiers in termite colonies: a list and a bibliography (Isoptera). Sociobiology 2:199–216

Haverty MI (1979) Soldier production and maintenance of soldier proportions in laboratory experimental groups of *Coptotermes formosanus* Shiraki. Insect Soc 26:69–84

Haverty MI, Howard RW (1981) Production of soldiers and maintenance of soldier proportions by laboratory experimental groups of *Reticulitermes flavipes* (Kollar) and *Reticulitermes virginicus* (Banks) (Isoptera: Rhinotermitidae). Insect Soc 28:32–39

Haverty MI, Thorne BL (1989) Agonistic behavior correlated with hydrocarbon phenotypes in dampwood termites, *Zootermopsis* (Isoptera: Termopsidae). J Insect Behav 2:523–543

Haverty MI, Page M, Nelson LJ, Blomquist GJ (1988) Cuticular hydrocarbons of dampwood termites, *Zootermopsis*: intra- and inter-colony variation and potential as taxonomic characters. J Chem Ecol 14:1035–1058

Haverty MI, Grace JK, Nelson LJ, Yamamoto RT (1996) Intercaste, intercolony, and temporal variation in cuticular hydrocarbons of *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae). J Chem Ecol 22:1813–1834

Haverty MI, Copren KA, Getty GM, Lewis VR (1999) Agonistic behavior and hydrocarbon phenotypes of colonies of *Reticulitermes* (Isoptera: Rhinotermitidae). Ann Entomol Soc Am 92:269–277

Haverty MI, Woodrow RJ, Nelson LJ, Grace JK (2000) Cuticular hydrocarbons of termites of the Hawaiian Islands. J Chem Ecol 26:1167–1191

Hayashi Y, Kitade O, Ji Kojima (2003) Parthenogenetic reproduction in neotenics of the subterranean termite *Reticulitermes speratus* (Isoptera, Rhinotermitidae). Entomol Sci 6:253–257

Hayashi Y, Lo N, Miuata H, Kitade O (2007) Sex-linked genetic influence on caste determination in a termite. Science 318:985–987

Heidecker JL, Leuthold RH (1984) The organisation of collective foraging in the harvester termite *Hodotermes mossambicus* (Isoptera). Behav Ecol Sociobiol 14:195–202

Hertel H, Hanspach A, Plarre R (2011) Differences in alarm responses in drywood and subterranean termites (Isoptera: Kalotermitidae and Rhinotermitidae) to physical stimuli. J Insect Behav 24:106–115

Hewitt PH, Watson JAL, Nel JCC, Schoeman I (1972) Control of the change from group to pair by *Hodotermes mossambicus* reproductives. J Insect Physiol 18:143–150

Himuro C, Yokoi T, Matsuura K (2011) Queen-specific volatile in a higher termite *Nasutitermes takasagoensis* (Isoptera: Termitidae). J Insect Physiol 57:962–965

Hinze B, Leuthold RH (1999) Age related polyethism and activity rhythms in the nest of the termite *Macrotermes bellicosus* (Isoptera, Termitidae). Insect Soc 46:392–397

Hinze B, Crailsheim K, Leuthold RH (2002) Polyethism in food processing and social organisation in the nest of *Macrotermes bellicosus* (Isoptera, Termitidae). Insect Soc 49:31–37

Howard RW, Blomquist GJ (2005) Ecological, behavioral and biochemical aspects of insect hydrocarbons. Annu Rev Entomol 50:371–393

Howard KJ, Thorne BL (2011) Eusocial evolution in termites and hymenoptera. In: Bignell DE, Roisin Y, Lo N (eds) Biology of termites: a modern synthesis. Springer, Dordrecht, pp 97–132

Howard RW, McDaniel CA, Blomquist GJ (1978) Cuticular hydrocarbons of the eastern subterranean termite, *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae). J Chem Ecol 4:233–245

Howard RW, McDaniel CA, Blomquist GJ (1980) Chemical mimicry as an integrating mechanism: cuticular hydrocarbons of a termitophile and its host. Science 210:431–433

Howard RW, McDaniel CA, Nelson DR et al (1982a) Cuticular hydrocarbons of *Reticulitermes virginicus* (Banks) and their role as potential species and caste-recognition cues. J Chem Ecol 8:1227–1239

Howard RW, McDaniel CA, Blomquist GJ (1982b) Chemical mimicry as an integrating mechanism for three termitophiles associated with *Reticulitermes virginicus* (Banks). Psyche 89:157–167

Howard RW, Thorne BL, Levings SC, McDaniel CA (1988) Cuticular hydrocarbons as chemotaxonomic characters for *Nasutitermes corniger* (Motschulsky) and *N. ephratae* (Holmgren) (Isoptera: Termitidae). Ann Entomol Soc Am 81:395–399

Howse PE (1964a) The significance of the sound produced by the termite *Zootermopsis angusticollis* (Hagen). Anim Behav 12:284–300

Howse PE (1964b) An investigation into the mode of action of the subgenual organ in the termite, *Zootermopsis angusticollis* Emerson, and in the cockroach, *Periplaneta americana* L. J Insect Physiol 10:409–424

Howse PE (1965) On the significance of certain oscillatory movements of termites. Insect Soc 12:335–346

Howse PE (1984) Alarm, defence and chemical ecology of social insects. In: Lewis T (ed) Insect communication. Academic Press, London, Orlando, pp 151–167

Hu XP, Song D, Gao X (2011) Biological changes in the Eastern subterranean termite, *Reticulitermes flavipes* (Isoptera, Rhinotermitidae) and its protozoa profile following starvation. Insect Soc 58:39–45

Huang Q, Guan C, Shen Q et al (2012a) Aggressive behavior and the role of antennal sensillae in the termite *Reticulitermes chinensis* (Isoptera: Rhinotermitidae). Sociobiology 59:1239–1251

Huang Q, Sun P, Zhou X, Lei C (2012b) Characterization of head transcriptome and analysis of gene expression involved in caste differentiation and aggression in *Odontotermes formosanus* (Shiraki). PLoS ONE 7(11):e50383

Hunt JH, Richard F-J (2013) Intracolony vibroacoustic communication in social insects. Insect Soc 60:403–417

Husseneder C, Grace JK (2001) Evaluation of DNA fingerprinting, aggression tests, and morphometry as tools for colony delineation of the Formosan subterranean termite. J Insect Behav 14:173–186

Husseneder C, Simms DM (2008) Size and heterozygosity influence partner selection in the Formosan subterranean termite. Behav Ecol 19:764–773

Husseneder C, Kaib M, Epplen C et al (1997) Small-scale population structure of the termite *Schedorhinotermes lamanianus*: aggression modulated by genetic and environmental factors. Mitt Dtsch Ges Allg Angew Entomol 11:183–187

Husseneder C, Brandl R, Epplen C et al (1998) Variation between and within colonies in the termite: morphology, genomic DNA, and behaviour. Mol Ecol 7:983–990

Inta R, Lai JCS, Fu EW, Evans TA (2007) Termites live in a material world: exploration of their ability to differentiate between food sources. J R Soc Interface 4:735–744

Inward DJG, Vogler AP, Eggleton P (2007a) A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. Mol Phyl Evol 44:953–967

Inward DJG, Beccaloni G, Eggleton P (2007b) Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. Biol Lett 3:331–335

Ishikawa Y, Miura T (2012) Hidden aggression in termite workers: plastic defensive behaviour dependent upon social context. Anim Behav 83:737–745

Jmhasly P, Leuthold RH (1999a) Intraspecific colony recognition in the termites *Macrotermes subhyalinus* and *Macrotermes bellicosus* (Isoptera, Termitidae). Insect Soc 46:164–170

Jmhasly P, Leuthold RH (1999b) The system of underground passages in *Macrotermes subhyalinus* and comparison of laboratory bioassays to field evidence of intraspecific encounters in *M. subhyalinus* and *M. bellicosus* (Isoptera, Termitidae). Insect Soc 46:332–340

Jmhasly P, Leuthold RH (1999c) Foraging territories of *Macrotermes bellicosus* and mutual territory dynamics between *M. bellicosus* and *M. subhyalinus* (Isoptera: Termitidae). Sociobiology 34:23–33

Johns PM, Howard KJ, Breisch NL et al (2009) Nonrelatives inherit colony resources in a primitive termite. Proc Natl Acad Sci USA 106:17452–17456

Jones DT, Eggleton P (2011) Global geography of termites: a compilation of sources. In: Bignell DE, Roisin Y, Lo N (eds) Biology of termites: a modern synthesis. Springer, Dordrecht, pp 477–498

Kaib M (1990) Intra- and interspecific chemical signals in the termite *Schedorhinotermes*—production sites, chemistry, and behaviour. In: Gribakin FG, Wiese K, Popov AV (eds) Sensory systems and communication in arthropods. Birkhauser Verlag, Basel, Boston & Berlin, pp 26–32

Kaib M, Brandl R (1992) Distribution, geographic variation and between-colony compatibility of *Schedorhinotermes lamanianus* in Kenya (Isoptera: Rhinotermitidae). In: Billen J (ed) Biology and evolution of social insects. Leuven University Press, Leuven, pp 121–131

Kaib M, Ziesmann J (1992) The labial gland in the termite *Schedorhinotermes lamanianus* (Isoptera: Rhinotermitidae): morphology and function during communal food exploitation. Insect Soc 39:373–384

Kaib M, Brandl R, Bagine RKN (1991) Cuticular hydrocarbon profiles: a valuable tool in termite taxonomy. Naturwissenschaften 78:176–179

Kaib M, Husseneder C, Epplen C et al (1996) Kin-biased foraging in a termite. Proc R Soc B 263:1527–1532

Kaib M, Franke S, Francke W, Brandl R (2002) Cuticular hydrocarbons in a termite: phenotypes and a neighbour-stranger effect. Physiol Entomol 27:189–198

Kaib M, Jmhasly P, Wilfert L et al (2004) Cuticular hydrocarbons and aggression in the termite *Macrotermes subhyalinus*. J Chem Ecol 30:365–385

Keller L, Nonacs P (1993) The role of queen pheromones in social insects: queen control or queen signal? Anim Behav 45:787–794

Kettler R, Leuthold RH (1995) Interspecific and intraspecific alarm response in the termite *Macrotermes subhyalinus* (Rambur). Insect Soc 42:145–156

Kirchner WH, Minkley N (2003) Nestmate discrimination in the harvester termite *Hodotermes mossambicus*. Insect Soc 50:222–225

Kirchner WH, Broecker I, Tautz J (1994) Vibrational alarm communication in the damp-wood termite *Zootermopsis nevadensis*. Physiol Entomol 19:187–190

Kitade O, Hayashi Y, Kikuchi Y, Kawarasaki S (2004) Distribution and composition of colony founding associations of a subterranean termite, *Reticulitermes kanmonensis*. Entomol Sci 7:1–8

Klochkov SG, Kozlovskii VI, Belyaeva NV (2005) Caste and population specificity of termite cuticule hydrocarbons. Chem Nat Compd 41:1–6

Kobayashi K, Hasegawas E, Yamamoto Y et al (2013) Sex ratio biases in termites provide evidence for kin selection. Nat Commun 4:2048

Korb J (2006) Limited food induces nepotism in drywood termites. Biol Lett 2:364–366

Korb J (2009) Termites: an alternative road to eusociality and the importance of group benefits in social insects. In: Gadau J, Fewell J (eds) Organization of insect societies—from genome to sociocomplexity. Harvard University Press, Cambridge, pp 128–147

Korb J, Heinze J (2008) Ecology of social evolution. Springer, Berlin

Korb J, Roux EA (2012) Why join a neighbour: fitness consequences of colony fusions in termites. J Evol Biol 25:2161–2170

Korb J, Schneider K (2007) Does kin structure explain the occurrence of workers in a lower termite? Evol Ecol 21:817–828

Korb J, Roux EA, Lenz M (2003) Proximate factors influencing soldier development in the basal termite *Cryptotermes secundus* (Hill). Insect Soc 50:299–303

Korb J, Weil T, Hoffmann K et al (2009) A gene necessary for reproductive suppression in termites. Science 324:758

Korb J, Buschmann M, Schafberg S et al (2012) Brood care and social evolution in termites. Proc R Soc B 279:2662–2671

Korman AK, Pashley DP, Haverty MI, La Fage JP (1991) Allozymic relationships among cuticular hydrocarbon phenotypes of *Zootermopsis* species (Isoptera: Termopsidae). Ann Entomol Soc Am 84:1–9

Kotoklo EA, Sillam-Dussès D, Ketoh G et al (2010) Identification of the trail-following pheromone of the pest termite *Amitermes evuncifer* (Isoptera: Termitidae). Sociobiology 55:579–588

Krasnec MO, Breed MD (2012) Eusocial evolution and the recognition systems in social insects. Adv Exp Med Biol 739:78–93

Krasulová J, Hanus R, Kutalová K et al (2012) Chemistry and anatomy of the frontal gland in soldiers of the sand termite *Psammotermes hybostoma* (Rhinotermitidae). J Chem Ecol 38:557–565

Krishna K, Grimaldi DA, Krishna V, Engel MS (2013) Treatise on the isoptera of the world. Bull Am Mus Nat Hist 377:1–200

Laduguie N, Robert A, Bonnard O et al (1994) Isolation and identification of (3*Z*,6*Z*,8*E*)-dodecatrien-1-ol in *Reticulitermes santonensis* Feytaud (Isoptera, Rhinotermitidae): roles in worker trail-following and in alate sex-attraction behavior. J Insect Physiol 40:781–787

Lainé LV, Wright DJ (2003) The life cycle of *Reticulitermes* spp. (Isoptera: Rhinotermitidae): what do we know? Bull Entomol Res 93:267–278

Lebrun D (1972) Effets de l'implantation de glandes mandibulaires sur la différenciation imaginale de *Calotermes flavicollis* Fabr. C R Acad Sci 274D:2077–2079

LeConte Y, Hefetz A (2008) Primer pheromones in social hymenoptera. Annu Rev Entomol 53:523–542

Lefeuve P, Bordereau C (1984) Soldier formation regulated by a primer pheromone from the soldier frontal gland in a higher termite, *Nasutitermes lujae*. Proc Natl Acad Sci USA 81:7665–7668

Legendre F, Whiting MF, Bordereau C et al (2008) The phylogeny of termites (Dictyoptera: Isoptera) based on mitochondrial and nuclear markers: implications for the evolution of the worker and pseudergate castes, and foraging behaviors. Mol Phyl Evol 48:615–627

Legendre F, Whiting MF, Grandcolas P (2013) Phylogenetic analyses of termite post-embryonic sequences illuminate caste and developmental pathway evolution. Evol Dev 15:146–157

Leis M, Sbrenna-Micciarelli A, Sbrenna G (1992) Communication in termites: preliminary observations on the vibratory movements of *Kalotermes flavicollis* (Fabr.) (Isoptera: Kalotermitidae). Ethol Ecol Evol 2:111–114

Leis M, Angelini I, Sbrenna-Micciarelli A, Sbrenna G (1994) Further observations on intercaste communication in *Kalotermes flavicollis*: frequence of vibratory movements under different experimental conditions. Ethol Ecol Evol 3:11–16

Leniaud L, Pichon A, Uva P, Bagnères A-G (2009) Unicoloniality in *Reticulitermes urbis*: a novel feature in a potentially invasive termite species. Bull Entomol Res 99:1–10

Leniaud L, Darrouzet E, Dedeine F et al (2011) Ontogenic potentialities of the worker caste in two subterranean termites. Evol Dev 13:138–148

Lenz M (1976) The dependence of hormone effects in termite caste determination on external factors. In: Lüscher M (ed) Phase and caste development in social insects (Endocrine aspects). Pergamon Press, Oxford, pp 73–89

Lenz M (1985) Is inter- and intra-specific variability of lower termite neotenic numbers due to adaptive thresholds for neotenic elimination? Considerations from studies on *Porotermes adamsoni* (Froggatt) (Isoptera: Termopsidae). Curr Themes Trop Sci 3:125–145

Leponce M, Roisin Y, Pasteels JM (1996) Intraspecific interactions in a community of arboreal nesting termites (Isoptera: Termitidae). J Insect Behav 9:799–817

Leuthold RH, Bruinsma O (1978) Pairing behavior in *Hodotermes mossambicus* (Isoptera). Psyche 84:109–119

Leuthold RH, Bruinsma O, Van Huis A (1976) Optical and pheromonal orientation and memory for homing distance in the harvester termite *Hodotermes mossambicus* (Hagen). Behav Ecol Sociobiol 1:127–139

Levings SC, Adams ES (1984) Intraspecific and interspecific territoriality in *Nasutitermes* (Isoptera: Termitidae) in a Panamanian mangrove forest. J Anim Ecol 53:705–714

Lewis VR, Nelson LJ, Haverty MI, Baldwin JA (2010) Quantitative changes in hydrocarbons over time in fecal pellets of *Incisitermes minor* may predict whether colonies are alive or dead. J Chem Ecol 36:1199–1206

Li G, Zou X, Lei C, Huang Q (2013) Antipredator behavior produced by heterosexual and homosexual tandem running in the termite *Reticulitermes chinensis* (Isoptera, Rhinotermitidae). Sociobiology 60:198–203

Liebig J, Eliyahu D, Brent CS (2009) Cuticular hydrocarbon profiles indicate reproductive status in the termite *Zootermopsis nevadensis*. Behav Ecol Sociobiol 63:1799–1807

Light SF (1944) Experimental studies on ectohormonal control of the development of supplementary reproductives in the termite genus *Zootermopsis* (formerly *Termopsis*). Univ Calif Pub Zool 53:1–40

Light SF, Weesner FM (1955) The production and replacement of soldiers in incipient colonies of *Reticulitermes hesperus* banks. Insect Soc 2:347–354

Lindström M, Norin T, Valterová I, Vrkoč J (1990) Chirality of the monoterpene alarm pheromones of termites. Naturwissenschaften 77:134–135

Lo N, Eggleton P (2011) Termite phylogenetics and co-cladogenesis with symbionts. In: Bignell DE, Roisin Y, Lo N (eds) Biology of termites: a modern synthesis. Springer, Dordrecht, pp 27–50

Lo N, Kitade O, Miura T et al (2004) Molecular phylogeny of the Rhinotermitidae. Insect Soc 51:365–371

Lo N, Hayashi Y, Kitade O (2009) Should environmental caste determination be assumed for termites? Am Nat 173:848–853

Long CE, Thorne BL (2006) Resource fidelity, brood distribution and foraging dynamics in complete laboratory colonies of *Reticulitermes flavipes* (Isoptera, Rhinotermitidae). Ethol Ecol Evol 18:113–125

Long CE, Thorne BL, Breisch NL (2003) Termite colony ontogeny: a long-term assessment of reproductive lifespan, caste ratios and colony size in *Reticulitermes flavipes* (Isoptera, Rhinotermitidae). Bull Entomol Res 93:439–445

Luchetti A, Dedeine F, Velonà A, Mantovani B (2013a) Extreme genetic mixing within colonies of the wood-dwelling termite *Kalotermes flavicollis* (Isoptera, Kalotermitidae). Mol Ecol 22:3391–3402

Luchetti A, Velonà A, Mueller M, Mantovani B (2013b) Breeding systems and reproductive strategies in Italian *Reticulitermes* colonies (Isoptera, Rhinotermitidae). Insect Soc 60:203–211

Lüscher M (1952) Die Production und Elimination von Ersatzgeschlechtstieren bei der Termite *Kalotermes flavicollis* Fabr. Z Vergl Physiol 34:123–141

Lüscher M (1955) Zur Frage der Übertragung socialer Wirkstoffe bei Termiten. Naturwissenschaften 42:186

Lüscher M (1956) Hemmende und fördernde Faktoren bei der Entstehung der Ersatzgeschlechtstiere bei der Termite *Kalotermes flavicollis* Fabr. Rev Suisse Zool 63:261–267

Lüscher M (1961) Social control of polymorphism in termites. Symp R Entomol Soc Lond 1:57–67

Lüscher M (1972) Environmental control of juvenile hormone (JH) secretion and caste differentiation in termites. Gen Comp Endocrinol 3:509–514

Lüscher M (1974) Kasten und Kastendifferenzierung bei niederen Termiten. In: Schmidt GH (ed) Sozialpolymorphismus bei Insekten. Wissenschaftliche Verlagsgesellschaft, Stuttgart, pp 694–739

Lys JA, Leuthold RH (1991) Task-specific distribution of the two worker castes in extranidal activities in *Macrotermes bellicosus* (Smeathman): observation of behaviour during food acquisition. Insect Soc 38:161–170

Maistrello L, Sbrenna G (1996) Frequency of some behavioural patterns in colonies of *Kalotermes flavicollis* (Isoptera Kalotermitidae): the importance of social interactions and vibratory movements as mechanisms for social integration. Ethol Ecol Evol 8:365–375

Mao L, Henderson G (2010) Group size effect on worker juvenile hormone titers and soldiers differentiation in Formosan subterranean termite. J Insect Physiol 56:725–730

Marins A, de Souza O (2008) Nestmate recognition in *Cornitermes cumulans* termites (Insecta: Isoptera). Sociobiology 51:255–263

Marten A, Kaib M, Brandl R (2009) Cuticular hydrocarbon phenotypes do not indicate cryptic species in fungus-growing termites (Isoptera: Macrotermitinae). J Chem Ecol 35:572–579

Matsuura K (2001) Nestmate recognition mediated by intestinal bacteria in a termite, *Reticulitermes speratus*. Oikos 92:20–26

Matsuura K (2005) Distribution of termite egg-mimicking fungi (“termite balls”) in *Reticulitermes* spp. (Isoptera: Rhinotermitidae) nests in Japan and the United States. Appl Entomol Zool 40:53–61

Matsuura K (2006) Termite-egg mimicry by a sclerotium-forming fungus. Proc R Soc B 273:1203–1209

Matsuura K (2011) Sexual and asexual reproduction in termites. In: Bignell DE, Roisin Y, Lo N (eds) Biology of termites: a modern synthesis. Springer, Dordrecht, pp 255–277

Matsuura K (2012) Multifunctional queen pheromone and maintenance of reproductive harmony in termite colonies. J Chem Ecol 38:746–754

Matsuura K, Kobayashi N (2007) Size, hatching rate, and hatching period of sexually and asexually eggs in the facultatively parthenogenetic termite *Reticulitermes speratus* (Isoptera: Rhinotermitidae). Appl Entomol Zool 42:241–246

Matsuura K, Nishida T (2001) Colony fusion in a termite: what makes the society “open”? Insect Soc 48:378–383

Matsuura K, Yamamoto Y (2011) Workers do not mediate the inhibitory power of queens in a termite, *Reticulitermes speratus* (Isoptera, Rhinotermitidae). Insect Soc 58:513–518

Matsuura K, Kobayashi N, Yashiro T (2007) Seasonal patterns of egg production in field colonies of the termite, *Reticulitermes speratus* (Isoptera: Rhinotermitidae). Popul Ecol 49:179–183

Matsuura K, Vargo EL, Kawatsu K et al (2009a) Queen succession through asexual reproduction in termites? Science 323:1687

Matsuura K, Yashiro T, Shimizu K et al (2009b) Cuckoo fungus mimics termite eggs by producing the cellulose-digesting enzyme β-glucosidase. Curr Biol 19:30–36

Matsuura K, Himuro C, Yokoi T et al (2010) Identification of a pheromone regulating caste differentiation in termites. Proc Natl Acad Sci USA 107:12963–12968

McMahan EA (1970) Polyethism in workers of *Nasutitermes costalis* (Holmgren). Insect Soc 17:113–120

Miller EM (1942) The problem of castes and caste differentiation in *Prorhinotermes simplex* (Hagen). Bull Univ Miami 15:3–27

Minkley N, Fujita AI, Brune A, Kirchner WH (2006) Nest specificity of the bacterial community in termite guts (*Hodotermes mossambicus*). Insect Soc 53:339–344

Misof B, Liu S, Meusemann K et al (2014) Phylogenomics resolves the timing and pattern of insect evolution. Science 346:763–767

Miura T, Matsumoto T (1995) Worker polymorphism and division of labor in the foraging behavior of the black marching termite *Hospitalitermes medioflavus*, on Borneo Island. Naturwissenschaften 82:564–567

Miura T, Matsumoto T (1998) Foraging organization of the open-air processional lichen-feeding termite *Hospitalitermes* (Isoptera: Termitidae) in Borneo. Insect Soc 45:17–32

Miura T, Scharf ME (2011) Molecular basis underlying caste differentiation in termites. In: Bignell DE, Roisin Y, Lo N (eds) Biology of termites: a modern synthesis. Springer, Dordrecht, pp 211–253

Miura T, Roisin Y, Matsumoto T (1998) Developmental pathways and polyethism of neuter castes in the processional nasute termite *Hospitalitermes medioflavus* (Isoptera: Termitidae). Zool Sci 15:843–848

Miyata H, Furuichi H, Kitade O (2004) Patterns of neotenic differentiation in a subterranean termite, *Reticulitermes speratus* (Isoptera: Rhinotermitidae). Entomol Sci 7:309–314

Mizumoto N, Matsuura K (2013) Colony-architecture of shelter tubes by termites. Insect Soc 60:525–530

Monnin T (2006) Chemical recognition of reproductive status in social insects. Ann Zool Fennici 43:515–530

Muller H, Korb J (2008) Male or female soldiers? An evaluation of several factors which may influence soldier sex ratio in lower termites. Insect Soc 55:213–219

Myles TG (1999) Review of secondary reproduction in termites (Insecta: Isoptera) with comments on its role in termite ecology and social evolution. Sociobiology 33:1–91

Myles TG, Chang F (1984) The caste system and caste mechanisms of *Neotermes connexus* (Isoptera: Kalotermitidae). Sociobiology 9:1–321

Nagin R (1972) Caste determination in *Neotermes jouteli* (Banks). Insect Soc 19:39–61

Nalepa CA, Evans TA, Lenz M (2011) Antennal cropping during colony foundation in termites. Zookeys 148:185–196

Nel JJC (1968) Aggressive behaviour of the harvester termites *Hodotermes mossambicus* (Hagen) and *Trinervitermes trinervoides* (Sjostedt). Insect Soc 15:156

Neoh KB, Indiran Y, Lenz M, Lee CY (2012) Does lack of intraspecific aggression or absence of nymphs determine acceptance of foreign reproductives in *Macrotermes*? Insect Soc 59:223–230

Nguyen TT, Kanaori K, Hojo MK et al (2011) Chemical identification and ethological function of soldier-specific secretion in Japanese subterranean termite *Reticulitermes speratus* (Rhinotermitidae). Biosci Biotechnol Biochem 75:1818–1822

Noirot C (1969) Glands and secretion. In: Krishna K, Weesner FM (eds) Biology of termites, vol 1. Academic Press, London and New York, pp 89–123

Noirot C (1982) La caste des ouvriers, élément majeur du succès évolutif des termites. Rivista Biol 75:157–195

Noirot C (1989) Social structure in termite societies. Ethol Ecol Evol 1:1–17

Nutting WL (1969) Flight and colony foundation. In: Krishna K, Weesner FM (eds) Biology of termites, vol 1. Academic Press, London and New York, pp 233–282

Ohta M, Matsuura F, Henderson G, Laine RA (2007) Novel free ceramides as components of the soldier defense gland of the Formosan subterranean termite (*Coptotermes formosanus*). J Lipid Res 48:656–664

Okot-Kotber BM (1985) Mechanisms of caste determination in a higher termite, *Macrotermes michaelseni* (Isoptera, Macrotermitinae). Curr Themes Trop Sci 3:267–306

Okot-Kotber BM, Ujváry I, Mollaaghababa R et al (1991) Physiological influence of fenoxycarb pro-insecticides and soldier head extracts of various termite species on soldier differentiation in *Reticulitermes flavipes* (Isoptera). Sociobiology 19:77–90

Oloo GW, Leuthold RH (1979) Influence of food on trail-laying and recruitment behavior in *Trinervitermes bettonianus* (Termitidae: Nasutitermitinae). Entomol Exp Appl 26:267–278

Olugbemi BO (2013) Intra- and inter-colonial agonistic behavior in the termite *Microcerotermes fuscotibialis* Sjostedt (Isoptera, Termitidae, Termitinae). J Insect Behav 26:69–78

Ozaki M, Wada-Katsumata A, Fujikawa K et al (2005) Ant nestmate and non-nestmate discrimination by a chemosensory sensillum. Science 309:311–314

Park YI, Raina A (2003) Factors regulating caste differentiation in the Formosan subterranean termite with emphasis on soldier formation. Sociobiology 41:49–60

Park YI, Raina AK (2005) Regulation of juvenile hormone titers by soldiers in the Formosan subterranean termite, *Coptotermes formosanus*. J Insect Physiol 51:385–391

Pearce MJ, Cowie RH, Pack AS, Reavey D (1990) Intraspecific aggression, colony identity and foraging distances in Sudanese *Microtermes* spp. (Isoptera: Termitidae: Macrotermitinae). Ecol Entomol 15:71–77

Peeters C, Liebig J (2009) Fertility signaling as a general mechanism of regulating reproductive division of labor in ants. In: Gadau J, Fewell J (eds) Organization of insect societies: from genome to socio-complexity. Harvard University Press, Cambridge, pp 220–242

Pellens R, D'Haese CA, Bellés X et al (2007) The evolutionary transition from subsocial to eusocial behavior in Dictyoptera: phylogenetic evidence for modification of the "shift-in-dependant-care" hypothesis with a new subsocial cockroach. Mol Phyl Evol 43:616–626

Peppuy A, Robert A, Sémon E et al (2001) (*Z*)-Dodec-3-en-1-ol, a novel termite trail pheromone identified after solid phase microextraction from *Macrotermes annandalei*. J Insect Physiol 47:445–453

Peppuy A, Robert A, Bordereau C (2004) Species-specific sex pheromones secreted from new sexual glands in two sympatric fungus-growing termites from northern Vietnam, *Macrotermes annandalei* and *M. barneyi*. Insect Soc 51:91–98

Perdereau E, Bagnères A-G, Dupont S, Dedeine F (2010a) High occurrence of colony fusion in a European population of the American termite *Reticulitermes flavipes*. Insect Soc 57:393–402

Perdereau E, Dedeine F, Christidès J-P, Bagnères A-G (2010b) Variations in worker cuticular hydrocarbons and soldier isoprenoid defensive secretions within and among introduced and native populations of the subterranean termite, *Reticulitermes flavipes*. J Chem Ecol 36:1189–1198

Perdereau E, Dedeine F, Christidès J-P et al (2011) Competition between invasive and indigenous species: an insular case study of subterranean termites. Biol Inv 13:1457–1470

Perdereau E, Bagnères A-G, Bankhead-Dronnet S et al (2013) Global genetic analysis reveals the putative native source of the invasive termite, *Reticulitermes flavipes*. Mol Ecol 22:1105–1119

Pichon A, Kutnik M, Leniaud L et al (2007) Development of experimentally orphaned termite worker colonies of two *Reticulitermes* species. Sociobiology 50:1200–1208

Pickens AL (1932) Observation on the genus *Reticulitermes* Holmgren. Pan-Pac Entomol 8:178–180

Piskorski R, Hanus R, Vašíčková S, Cvačka J, Šobotník J, Svatoš A, Valterová I (2007) Nitroalkenes and sesquiterpene hydrocarbons from the frontal gland of three *Prorhinotermes* termite species. J Chem Ecol 33:1787–1794

Piskorski R, Hanus R, Kalinová B et al (2009) Temporal and geographic variations in the morphology and chemical composition of the frontal gland in imagoes of *Prorhinotermes* species (Isoptera: Rhinotermitidae): geographic and temporal variations. Biol J Linnean Soc 98:384–392

Polizzi JM, Forschler BT (1999) Factors that affect aggression among the worker caste of *Reticulitermes* spp. subterranean termites (Isoptera: Rhinotermitidae). J Insect Behav 12:133–146

Prestwich GD, Robles S, Mohamed M (1987) Biochemical basis for caste differentiation in termites. In: Eder J, Rembold H (eds) Chemistry and biology of social insects. Verlag J. Peperny, Munchen, pp 314–315

Quennedey A, Peppuy A, Courrent A et al (2004) Ultrastructure of posterior sternal glands of *Macrotermes annandalei* (Silvestri): new members of the sexual glandular set found in termites (Insecta). J Morphol 262:683–691

Quennedey A, Sillam-Dussès D, Robert A, Bordereau C (2008) The fine structural organization of sternal glands of pseudergates and workers in termites (Isoptera): a comparative survey. Arthropod Struct Dev 37:168–185

Quintana A, Reinhard J, Faure R et al (2003) Interspecific variation in terpenoid composition of defensive secretions of European *Reticulitermes* termites. J Chem Ecol 39:639–652

Raina AK, Bland JM, Dickens JC et al (2003) Premating behavior of dealates of the Formosan subterranean termite and evidence for the presence of a contact sex pheromone. J Insect Behav 16:233–245

Ratnieks FLW, Foster KR, Wenseleers T (2006) Conflict resolution in insect societies. Annu Rev Entomol 51:581–608

Reinhard J, Clément J-L (2002) Alarm reaction of European *Reticulitermes* termites to soldier head capsule volatiles (Isoptera, Rhinotermitidae). J Chem Ecol 15:95–107

Reinhard J, Kaib M (1995) Interaction of pheromones during food exploitation by the termite *Schedorhinotermes lamanianus*. Physiol Entomol 20:266–272

Reinhard J, Kaib M (2001a) Trail communication during foraging and recruitment in the subterranean termite *Reticulitermes santonensis* De Feytaud (Isoptera, Rhinotermitidae). J Insect Behav 14:157–171

Reinhard J, Kaib M (2001b) Food exploitation in termites: Indication for a general feeding-stimulating signal in labial gland secretion of isoptera. J Chem Ecol 27:189–201

Reinhard J, Hertel H, Kaib M (1997a) Systematic search for food in the subterranean termite *Reticulitermes santonensis* De Feytaud (Isoptera, Rhinotermitidae). Insect Soc 44:147–158

Reinhard J, Hertel H, Kaib M (1997b) Feeding stimulating signal in labial gland secretion of the subterranean termite *Reticulitermes santonensis*. J Chem Ecol 23:2371–2381

Reinhard J, Lacey MJ, Ibarra F et al (2002) Hydroquinone: a general phagostimulating pheromone in termites. J Chem Ecol 28:1–14

Reinhard J, Quintana A, Sreng L, Clément J-L (2003) Chemical signals inducing attraction and alarm in European *Reticulitermes* termites (Isoptera, Rhinotermitidae). Sociobiology 42:675–691

Renoux J (1976) Le polymorphisme de *Schedorhinotermes lamanianus* (Sjöstedt) (Isoptera: Rhinotermitidae). Insect Soc 23:279–494

Richard F-J, Hunt JH (2013) Intracolony chemical communication in social insects. Insect Soc 60:275–291

Röhrig A, Kirchner WH, Leuthold RH (1999) Vibrational alarm communication in the African fungus-growing termite genus *Macrotermes* (Isoptera, Termitidae). Insect Soc 46:71–77

Roisin Y, Korb J (2011) Social organisation and the status of workers in termites. In: Bignell DE, Roisin Y, Lo N (eds) Biology of termites: a modern synthesis. Springer, Dordrecht, pp 133–164

Roisin Y, Everaerts C, Pasteels JM, Bonnard O (1990) Caste-dependent reactions to soldier defensive secretion and chiral alarm/recruitment pheromone in *Nasutitermes princeps*. J Chem Ecol 16:2865–2875

Rojas MG, Werle C, Cottrell N, Morales-Ramos JA (2005) Changes in the ratios of four cuticular hydrocarbons in Formosan subterranean termite workers (*Coptotermes formosanus*) (Isoptera: Rhinotermitidae) due to diet. Sociobiology 46:131–140

Rosengaus RB, Jordan C, Lefebvre ML, Traniello JFA (1999) Pathogen alarm behavior in a termite: a new form of communication in social insects. Naturwissenschaften 86:544–548

Rosengaus RB, Levebvre ML, Traniello JFA (2000) Inhibition of fungal spore germination by *Nasutitermes*: evidence for a possible antiseptic role of soldier defensive secretions. J Chem Ecol 26:21–39

Runcie CD (1987) Behavioral evidence for multicomponent trail pheromone in the termite, *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae). J Chem Ecol 13:1967–1978

Rupf T, Roisin Y (2008) Coming out of the woods: do termites need a specialized worker caste to search for new food sources? Naturwissenschaften 95:811–819

Sands WA (1982) Agonistic behavior of African soldierless Apicotermitinae (Isoptera: Termitidae). Sociobiology 7:61–72

Saran RK, Millar JG, Rust MK (2007) Role of (3*Z,6Z,8E*)-dodecatrien-1-ol in trail following, feeding, and mating behavior of *Reticulitermes hesperus*. J Chem Ecol 33:369–389

Sbrenna G, Sbrenna-Micciarelli A, Leis M, Pavan G (1992) Vibratory movements and sound production in *Kalotermes flavicollis* (Isoptera: Kalotermitidae). In: Billen J (ed) Biology and evolution of social insects. Leuven University Press, Leuven, pp 233–238

Scharf ME, Wu-Scharf D, Pittendrigh BR et al (2003) Caste- and development-associated gene expression in a lower termite. Genom Biol 4:R62

Schedel A, Kaib M (1987) Polyethism during foraging in *Schedorhinotermes lamanianus* in unprotected areas: the role of exocrine glands. In: Eder J, Rembold H (eds) Chemistry and biology of social insects. Verlag J. Peperny, Munich, p 416

Schinghammmer MA, Zhou X, Kambhampati S et al (2011) A novel gene from the takeout family involved in termite trail-following behavior. Gene 474:12–21

Schuurman G, Dangerfield JM (1995) Assessment of intraspecific aggression in *Macrotermes michaelseni* (Isoptera: Macrotermitinae). Sociobiology 26:33–38

Schwander T, Lo N, Beekman M et al (2010) Nature versus nurture in social insect caste differentiation. Trend Ecol Evol 25:275–282

Sen R, Raychoudhury R, Cai Y et al (2013) Differential impacts of juvenile hormone, soldier head extract and alternate caste phenotypes on host and symbiont transcriptome composition in the gut of the termite *Reticulitermes flavipes*. BMC Genom 14:491

Sevala VL, Bagnères A-G, Kuenzli M et al (2000) Cuticular hydrocarbons of the dampwood termite, *Zootermopsis nevadensis*: caste differences and role of lipophorin in transport of hydrocarbons and hydrocarbon metabolites. J Chem Ecol 26:765–789

Shellman-Reeve JS (1994) Limited nutrients in a dampwood termite: nest preference, competition and cooperative nest defence. J Anim Ecol 63:921–932

Shellman-Reeve JS (1997) The spectrum of eusociality in termites. In: Choe JC, Crespi BJ (eds) The evolution of social behaviour in insects and arachnids. Cambridge University Press, Cambridge, pp 52–93

Shellman-Reeve JS (1999) Courting strategies and conflicts in a monogamous, biparental termite. Proc R Soc B 266:137–144

Shellman-Reeve JS (2001) Genetic relatedness and partner preference in a monogamous, wood-dwelling termite. Anim Behav 61:869–876

Shelton TG, Grace JK (1996) Review of agonistic behaviors in the Isoptera. Sociobiology 28:155–176

Sillam-Dussès D, Sémon E, Lacey MJ et al (2007) Trail-following pheromones in basal termites, with special reference to *Mastotermes darwiniensis*. J Chem Ecol 33:1960–1977

Sillam-Dussès D, Kalinová B, Jiroš P et al (2009a) Identification by GC-EAD of the two-component trail-following pheromone of *Prorhinotermes simplex* (Isoptera, Rhinotermitidae, Prorhinotermitinae). J Insect Physiol 55:751–757

Sillam-Dussès D, Sémon E, Robert A, Bordereau C (2009b) (*Z*)-Dodec-3-en-1-ol, a common major component of the trail-following pheromone in the termites *Kalotermitidae*. Chemoecology 19:103–108

Sillam-Dussès D, Sémon E, Robert A et al (2010) Identification of multi-component trail pheromones in the most evolutionarily derived termites, the Nasutitermitinae (Termitidae). Biol J Linnean Soc 99:20–27

Sillam-Dussès D, Krasulová J, Vrkoslav V et al (2012) Comparative study of the labial gland secretion in termites (Isoptera). PLoS ONE 7(10):e46431

Simpson SJ, Sword GA, Lo N (2011) Polyphenism in insects. Curr Biol 21:738–749

Singer TL (1998) Roles of hydrocarbons in the recognition systems of insects. Amer Zool 38:394–405

Smith AA, Hölldobler B, Liebig J (2009) Cuticular hydrocarbons reliably identify cheaters and allow enforcement of altruism in a social insect. Curr Biol 19:78–81

Šobotník J, Weyda F, Hanus R (2003) Ultrastructure of epidermal glands in neotenic reproductives of the termite *Prorhinotermes simplex* (Isoptera: Rhinotermitidae). Arthropod Struct Dev 32:201–208

Šobotník J, Hanus R, Kalinová B et al (2008) (E, E)-α-Farnesene, an alarm pheromone of the termite Prorhinotermes canalifrons. J Chem Ecol 34:478–486

Šobotník J, Jirošová A, Hanus R (2010) Chemical warfare in termites. J Insect Physiol 56:1012–1021

Šobotník J, Bourguignon T, Hanus R et al (2012) Explosive backpacks in old termite workers. Science 337:436

Springhetti A (1970) Influence of the king and queen on the differentiation of soldiers in *Kalotermes flavicollis* Fabr. (Isoptera). Monitore Zool Ital 4:99–105

Stuart AM (1963) Studies on the communication of alarm in the termite *Zootermopsis nevadensis* (Hagen), Isoptera. Physiol Zool 36:85–96

Stuart AM (1967) Alarm, defense, and construction behavior relationships in termites (Isoptera). Science 156:1123–1125

Stuart AM (1979) The determination and regulation of the neotenic reproductive caste in the lower termites (Isoptera): with special reference to the genus *Zootermopsis* (Hagen). Sociobiology 4:223–237

Stuart AM (1981) The role of pheromones in the initiation of foraging, recruitment and defence by the soldiers of a tropical termite, *Nasutitermes corniger* (Motschulsky). Chem Senses 6:409–420

Stuart AM (1988) Preliminary studies on the significance of head-banging movements in termites with special reference to *Zootermopsis angusticollis* (Hagen) (Isoptera: Hodotermitidae). Sociobiology 14:49–60

Su NY, Haverty MI (1991) Agonistic behavior among colonies of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae), from Florida and Hawaii: lack of correlation with cuticular hydrocarbon composition. J Insect Behav 4:115–128

Sun Q, Zhou X (2013) Corpse management in social insects. Int J Biol Sci 9:313–321

Sutton PA, Wilde MJ, Martin SJ et al (2013) Studies of long chain lipids in insects by high temperature gas chromatography and high temperature gas chromatography-mass spectrometry. J Chromatogr A 1297:236–240

Takahashi S, Gassa A (1995) Roles of cuticular hydrocarbons in intra- and inter-specific recognition behavior of two Rhinotermitidae species. J Chem Ecol 21:1837–1845

Takematsu Y, Kambara K (2012) Nestmate recognition and cuticular hydrocarbons of two sympatric species of *Reticulitermes* in Japan (Isoptera: Rhinotermitidae). Sociobiology 59:1205–1215

Takematsu Y, Yamaoka R (1997) Taxonomy of *Glyptotermes* (Isoptera, Kalotermitidae) in Japan with reference to cuticular hydrocarbon analysis as chemotaxonomic characters. Esakia 37:1–14

Tarver MR, Schmelz EA, Rocca JR et al (2009) Effects of soldier-derived terpenes on soldier caste differentiation in the termite *Reticulitermes flavipes*. J Chem Ecol 35:256–264

Tarver MR, Zhou X, Scharf ME (2010) Socio-environmental and endocrine influences on developmental and caste-regulatory gene expression in the eusocial termite *Reticulitermes flavipes*. BMC Mol Biol 11:28

Tarver MR, Schmelz EA, Scharf ME (2011) Soldier caste influences on candidate primer phreromone levels and juvenile hormone-dependent caste differentiation in workers of the termite *Reticulitermes flavipes*. J Insect Physiol 57:771–777

Thorne BL (1982) Termite-termite interactions: workers as an agonistic caste. Psyche 89:133–150

Thorne BL, Haverty MI (1991) A review of intracolony, intraspecific, and interspecific agonism in termites. Sociobiology 19:115–145

Thorne BL, Page M (1990) Surface hydrocarbon components of two species of *Nasutitermes* from Trinidad. J Chem Ecol 16:2441–2450

Thorne BL, Traniello JFA (2002) Comparative social biology of basal taxa of ants and termites. Annu Rev Entomol 48:283–306

Thorne BL, Traniello JFA, Adam ES et al (1999) Reproductive dynamics and colony structure of subterranean termites of the genus *Reticulitermes* (Isoptera, Rhinotermitidae): a review of the evidence from behavioral, ecological, and genetic studies. Ethol Ecol Evol 11:149–169

Thorne BL, Breisch NL, Muscedere ML (2003) Evolution of eusociality and the soldier caste in termites: influence of intraspecific competition and accelerated inheritance. Proc Natl Acad Sci USA 100:12808–12813

Traniello JFA (1981) Enemy deterrence in the recruitment strategy of a termite: soldier-organized foraging in *Nasutitermes costalis*. Proc Natl Acad Sci USA 78:1976–1979

Traniello JFA (1982) Recruitment and orientation components in a termite trail pheromone. Naturwissenschaften 69:343–345

Traniello JFA, Beshers SN (1985) Species-specific alarm recruitment responses in a neotropical termite. Naturwissenschaften 72:491–492

Traniello JFA, Busher C (1985) Chemical regulation of polyethism during foraging in the neotropical termite *Nasutitermes costalis*. J Chem Ecol 11:319–332

Traniello JFA, Leuthold RH (2000) Behavior and ecology of foraging in termites. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, London, pp 141–168

Tsunoda K, Matsuoka H, Yoshimura T et al (1999) Foraging populations and territories of *Reticulitermes speratus* (Isoptera: Rhinotermitidae). J Econ Entomol 92:604–609

Uva P, Clément J-L, Bagnères A-G (2004a) Colonial and geographic variations in agonistic behaviour, cuticular hydrocarbons and mtDNA of Italian populations of *Reticulitermes lucifugus* (Isoptera, Rhinotermitidae). Insect Soc 51:163–170

Uva P, Clément J-L, Austin JW et al (2004b) Origin of a new *Reticulitermes* termite (Isoptera, Rhinotermitidae) inferred from mitochondrial and nuclear DNA data. Mol Phyl Evol 30:344–353

Valterová I, Křeček J, Vrkoč J (1989) Intraspecific variation in the defence secretions of *Nasutitermes ephratae* soldiers and the biological activity of some of their components. Biochem Syst Ecol 17:327–332

Valterová I, Vrkoč J, Lindström M, Norin T (1992) On the natural occurrence of (-)3-carene, a component of termite defense. Naturwissenschaften 79:416–417

Valterová I, Vrkoč J, Norin T (1993) The enantiomeric composition of monoterpene hydrocarbons in the defensive secretions of *Nasutitermes* termites (Isoptera): inter- and intraspecific variations. Chemoecology 4:120–123

Van Oystaeyen A, Caliari Oliviera R et al (2014) Conserved class of queen pheromoens stops social insect workers from reproducting. Science 343:287–290

Van Zweden JS, d'Ettorre P (2010) Nestmate recognition in social insects and the role of hydrocarbons. In: Blomquist GJ, Bagnères A-G (eds) Insect hydrocarbons: biology, biochemistry, and chemical ecology. Cambridge University Press, Cambridge, pp 222–243

Vargo EL (2000) Polymorphism at trinucleotide microsatellite loci in the subterranean termite *Reticulitermes flavipes*. Mol Ecol 9:817–820

Vargo EL, Henderson G (2000) Identification of polymorphic microsatellite loci in the Formosan subterranean termite *Coptotermes formosanus* Shiraki. Mol Ecol 9:1935–1938

Vargo EL, Husseneder C (2009) Biology of subterranean termites: insights from molecular studies of *Reticulitermes* and *Coptotermes*. Annu Rev Entomol 54:379–403

Vargo EL, Husseneder C (2011) Genetic structure of termite colonies and populations. In: Bignell DE, Roisin Y, Lo N (eds) Biology of termites: a modern synthesis. Springer, Dordrecht, pp 133–164

Vargo EL, Labadie PE, Matsuura K (2012) Asexual queen succession in the subterranean termite *Reticulitermes virginicus*. Proc R Soc London B 279:813–819

Vargo EL, Leniaud L, Swoboda LE et al (2013) Clinal variation in colony breeding structure and level of inbreeding in the subterranean termites *Reticulitermes flavipes* and *R. grassei*. Mol Ecol 22:1447–1462

Vasquez GM, Schal C, Silverman J (2009) Colony fusion in Argentine ants is guided by workers and queen cuticular hydrocarbon profile similarity. J Chem Ecol 35:922–932

Vauchot B, Provost E, Bagnères A-G et al (1996) Regulation of the chemical signatures of two termite species, *Reticulitermes santonensis* and *R.* (*l.*) *grassei*, living in mixed colonies. J Insect Physiol 42:309–321

Vauchot B, Provost E, Bagnères A-G et al (1998) Differential adsorption of allospecific hydrocarbons by the cuticles of two termite species, *Reticulitermes santonensis* and *R. lucifugus grassei*, living in a mixed colony. J Insect Physiol 44:59–66

Vrkoč J, Křeček J, Hrdý I (1978) Monoterpenic alarm pheromones in two *Nasutitermes* species. Acta Entomol Bohemoslov 75:1–8

Watanabe D, Gotoh H, Miura T et al (2011) Soldier presence suppresses presoldier differentiation through a rapid decrease of JH in the termite *Reticulitermes speratus*. J Insect Physiol 57:791–795

Watson JAL, McMahan EA (1978) Polyethism in the Australian harvester termite *Drepanotermes* (Isoptera, Termitinae). Insect Soc 25:53–62

Wei JQ, Mo JC, Pan CY et al (2007) The intestinal microbes inducing the agonistic behavior of inter-colonial individuals in *Coptotermes formosanus* (Isoptera: Rhinotermitidae). Sociobiology 50:245–256

Weil T, Rehli M, Korb J (2007) Molecular basis for the reproductive division of labour in a lower termite. BMC Genomics 8

Weil T, Hoffmann K, Kroiss J et al (2009a) Scent of a queen-cuticular hydrocarbons specific for female reproductives in lower termites. Naturwissenschaften 96:315–319

Weil T, Korb J, Rehli M (2009b) Comparison of queen-specific gene expression in related lower termite species. Mol Biol Evol 26:1841–1850

Wheeler MW, Tarver MR, Coy MR et al (2010) Characterization of four esterase genes and esterase activity from the gut of the termite *Reticulitermes flavipes*. Archiv Insect Biochem Physiol 73:30–48

Wilson DS, Clark AB (1977) Above ground predator defence in the harvester termite, *Hodotermes mossambicus* (Hagen). J Ent Soc Sthn Africa 40:271–282

Wilson-Rich N, Spivak M, Fefferman NH, Starks PT (2009) Genetic, individual, and group facilitation of disease resistance in insect societies. Annu Rev Entomol 54:405–423

Wolfrum U, Kaib M (1988) Kastenspezifisches Verhalten der Termite *Schedorhinotermes lamanianus* und dessen Beziehung zu Unterschieden in Ultrastruktur, Haufigkeit und Topographie antennaler Sensillen. Mitt Dtsch Ges Allg Angew Entomol 6:86–90

Woodrow RJ, Grace JK, Nelson LJ, Haverty MI (2000) Modification of cuticular hydrocarbons of *Cryptotermes brevis* (Isoptera: Kalotermitidae) in response to temperature and relative humidity. Environ Entomol 29:1100–1107

Yamamoto Y, Matsuura K (2011) Queen pheromone regulates egg production in a termite. Biol Lett 7:727–729

Yamamoto Y, Kobayashi T, Matsuura K (2012) The lack of chiral specificity in a termite queen pheromone. Physiol Entomol 37:192–195

Yashiro T, Matsuura K (2007) Distribution and phylogenic analysis of termite egg-mimicking fungi “termite balls” in *Reticulitermes* termites. Ann Entomol Soc Am 100:532–538

Zalkow LH, Howard RH, Gelbaum LT et al (1981) Chemical ecology of *Reticulitermes flavipes* (Kollar) and *R. virginicus* (Banks): chemistry of the soldier cephalic secretions. J Chem Ecol 7:717–731

Zhang S, Mo J, Teng L et al (2006) Inter-colonial variation in the compositions of the frontal gland secretions of *Coptotermes formosanus* (Isoptera: Rhinotermitidae). Sociobiology 47:553–561

Zhao CJ, Rickards RW, Trowell SC (2004) Antibiotics from Australian terrestrial invertebrates. Part 1: antibacterial trinervitadienes from the termite *Nasutitermes triodiae*. Tetrahedron 60:10753–10759

Zhou X, Oi FM, Scharf ME (2006) Social exploitation of hexamerin: RNAi reveals a major caste-regulatory factor in termites. Proc Natl Acad Sci USA 103:4499–4504

Zhu F, Xu P, Barbosa RME et al (2013) RNAi-based demonstration of direct link between specific odorant receptors and mosquito oviposition behavior. Insect Biochem Mol Biol 43:916–923

Zimmermann RB (1983) Sibling manipulation and indirect fitness in termites. Behav Ecol Sociobiol 12:143–145

Chapter 12
Recognition and Family Life: Recognition Mechanisms in the Biparental Burying Beetle

Sandra Steiger

Abstract Burying beetles (genus *Nicrophorus*) are one of the few insect taxa that provide elaborate prehatching and posthatching biparental care. They reproduce on dead vertebrates and both parents are known to feed and defend their young. In this chapter, I will show that both of their key characteristics, their extended biparental care as well as their reproduction on a valuable and sought-after resource gave rise to the evolution of sophisticated recognition mechanisms. They are able to recognize the sex of a conspecific, their previous mating partner, their breeding partner including its reproductive sate and—using temporal cues—their offspring. I will provide an overview of the recent advances in elucidating the recognition processes of burying beetles and will demonstrate that most of the recognition mechanisms are mediated by chemical cues and signals.

Keywords Burying beetle · *Nicrophorus* · Biparental care · Chemical signals · Parent-offspring interactions

Introduction

The larva is begging for food by raising its head while waving its legs and touching the mother's mouthpart. Its mother is responding by regurgitating predigested carrion food, while the father is just chasing off an intruder intending to kill the brood. This description reflects a typical family life in burying beetles (Coleoptera: Silphidae: *Nicrophorus*) and illustrates the importance of recognition processes in insect species exhibiting extended parental care.

S. Steiger (✉)
Institute of Evolutionary Ecology and Conservation Genomics, University of Ulm,
Albert-Einstein-Allee 11, 89081 Ulm, Germany
e-mail: sandra.steiger@uni-ulm.de

L. Aquiloni and E. Tricarico (eds.), *Social Recognition in Invertebrates*,
DOI 10.1007/978-3-319-17599-7_12

Family life is crucially dependent on recognition mechanisms as parents have to recognize their offspring, offspring their parents and in the case of biparental care, the breeding partners each other. Certainly, the recognition mechanisms involved might not necessarily be very sophisticated in many species: offspring, for example, can be indirectly recognized by correctly identifying the nest or burrow. The degree of complexity of the recognition system also strongly depends on the encounter rate with undesirable senders, i.e. brood parasites or rivals that try to steal or take-over important resources necessary to raise the brood. If there is a very low risk of encountering them, the recognition system might be not very fine tuned. However, in systems in which parents defend or provide a valuable resource (i.e. provide parental care), cheats, who attempt to acquire the resource, are selected for and brood parasites are usually found to be common (see e.g. Kilner and Langmore 2011). This in turn selects for recognition processes in parents to identify and reject the parasites. A co-evolutionary arms race between host and parasite eventually leads to very fine tuned and complex recognitions system. Consequently, in species with parental care, we would expect more elaborate forms of recognition processes than in species not engaging in any kind of social behavior. For that reason, it is not surprising that burying beetles, which are well-known for their extended biparental care of young, have evolved a rather complex recognition system.

Nicrophorus is a northern hemisphere genus comprising about 72 species (Sikes and Venables 2013; Peck and Kaulbars 1987). Their peculiar habit to bury small vertebrate carcasses, mice or birds, as food for their larvae has fascinated scientists for centuries (e.g. Pukowski 1933; Scott 1998; Eggert and Müller 1997; Royle et al. 2013; Walling et al. 2008; Trumbo and Robinson 2004; Cotter et al. 2010; Steiger 2013; Suzuki and Nagano 2009; Fabre 1899). Usually it is a pair of beetle, a male and a female, which bury a corpse, thereby rolling it up into a ball, removing fur or feathers (Pukowski 1933) and treating it with antimicrobial oral and anal secretion to defend the carcass against competing microorganisms (e.g. Arce et al. 2012; Cotter and Kilner 2009; Suzuki 2001; Hall et al. 2011; Steiger et al. 2011a). The female lays her eggs singly in the surrounding soil and after the larvae have hatched they crawl to the carcass (Pukowski 1933). The parents prepare the carrion ball by opening a small feeding depression at the top, where the larvae usually aggregate. At this time the feeding of the larvae with predigested carrion food begins. The larvae show a specialized begging behavior in which they rear up and wave their legs to obtain food from their parents (Rauter and Moore 1999; Smiseth et al. 2003). Both parents engage in feeding, however, females spend more time nourishing, whereas males are more involved in defending the carcass from competitors (Fetherston et al. 1990; Trumbo 2006). Larvae are also able to self-feed directly from the carcass and the older they grow, the less time they spent begging and the more time feeding on their own. The female stays on the carcass until larval development is complete, the male usually leaves a few days earlier than the female (Trumbo 1991; Bartlett 1988; Scott and Traniello 1990). The larvae crawl into the surrounding soil for pupation and a few weeks after, adult emergence takes place (Pukowski 1933). However, in some species, larvae stay in the soil as prepupae, and adults do not emerge until the following summer (Eggert and Müller 1997).

Vertebrate carrion is a rare and ephemeral resource, but because of its high nutritive value, extraordinary valuable and sought-after. Not surprisingly, a carcass often attracts many animals, and—to be able to use it for one's own reproduction—burying beetles have to defend it against intra- and interspecific competitors as well as to find appropriate mating and breeding partners (Eggert and Müller 1997; Scott 1998). Even buried carcasses have to be protected against hetero- and conspecifics that try to kill the brood and use the resource for their own reproduction (Trumbo 1990a, 1994; Robertson 1993; Scott 1990). Moreover, intraspecific brood parasitism is known to occur: competitively inferior females do not always leave the carcass immediately, but may stay near the carcass and lay eggs of their own (Müller et al. 1990). Hence, discrimination against unrelated young should be selectively favored to avoid wasting resources on foreign offspring. It goes without saying that recognition is a necessary skill for burying beetles to either effectively defend the carcass, to mate with appropriate partners or to care for their own offspring. For the diverse task they have evolved an indirect time dependent recognition system as well as different social recognition systems, from familiar and class level recognition to nearly true individual recognition (see Gherardi et al. 2012 for definition of social recognition systems). In some cases, they appear to have innate representations of the cues of desired individuals, in other cases they learn the cues of senders and use the memory as a template afterwards in their discrimination decisions. Although burying beetles are known to produce sounds through stridulation during fights, prior to mating and during offspring feeding (Pukowski 1933; Niemitz and Krampe 1972; Huerta et al. 1992), all direct recognition mechanisms investigated to date are mediated by chemical cues and signals. Burying beetles release a vast array of chemicals: they possess a complex mixture of lipids on their cuticle (Steiger et al. 2007) and they also emit more volatile substances into the surroundings (Haberer et al. 2008, 2010).

In this chapter, I provide an overview of the recent advances in elucidating the social recognition processes of burying beetles. I start with the most fundamental type of recognition, the recognition of mating partners (i.e. recognition of species and sex), then I proceed with the more special features of burying beetles, the recognition of breeding partners and parent-offspring recognition.

Recognition Mechanisms Between the Sexes

Long-Range Mate Recognition

It has long been known that male burying beetles release a volatile sex pheromone, thereby adopting a headstand-like posture, pointing their head down and raising the abdomen (Pukowski 1933). Males engage in pheromone emission after having found a carcass suitable for reproduction as well as in the absent of a carcass, in a daily routine towards the end of the species-typical daily activity period (Eggert and Müller 1989b; Müller and Eggert 1987; Beeler et al. 1999). Females recognize the species-specific pheromone and are attracted to it from a distance. They appear not to be able to discriminate between resource owner and non-owner: a field study has shown that males that have buried a carcass prior to pheromone emission are equally effective in attracting females as males that have not (Eggert and Müller 1989a). Even if the males are not in the possession of a carcass, females are not reluctant but will accept copulation, although they usually fly off after one mating event (Eggert and Müller 1989a). In this situation, females do not gain a resource for reproduction, but they may still benefit by gaining fresh sperm that enables them to reproduce alone in the case they find a carcass suitable for reproduction later on. Interestingly, also conspecific males respond to the sex pheromone, most likely because there might be a chance to take over a carcass from the calling male or to mate with surplus females the pheromone emitter attracts (Müller and Eggert 1987). The sex ratio of the attracted beetle is, however, usually biased towards females. The opportunity to take-over a resource might also explain the asymmetric heterospecific cross-attraction that can be observed in field studies: larger, and therefore in a fight superior *Nicrophorus* species eavesdrop on and react to the male sex pheromone of smaller species, but not vice versa (Haberer et al. 2011; Müller and Eggert 1987). The larger *Nicrophorus humator*, for example, is attracted to its own as well as to the sex pheromone of the smaller *Nicrophorus vespilloides*, whereas *N. vespilloides* does not respond to the sex pheromone of *N. humator* and is exclusively attracted by its own male pheromone (Haberer et al. 2011). Although all burying beetles studied to date are known to release a sex pheromone, only the sex attractants of *N. vespilloides* and *N. humator* have been identified yet. Both species release an ester, the first species ethyl 4-methylheptanoate (Haberer et al. 2008), the second methyl 4-methyloctanoate (Haberer et al. 2011).

Whether females extract more information from the male sex pheromone, beyond species and sex, is not very well investigated. There is only one study that had looked into this topic: Beeler et al. (2002) has shown that female *Nicrophorus orbicollis* discriminate males of different body sizes from a distance preferring males of larger size. However, as the pheromone of *N. orbicollis* has not identified yet, it is not clear, whether this preference is based on quantitative or qualitative differences in the sex attractant.

Short-Range Mate Recognition

A vertebrate carcass as well as a burying beetle's sex pheromone often attracts several beetles of both sexes (Eggert and Müller 1989b; Müller and Eggert 1987). Hence, the long range sex pheromone is not enough to guarantee an appropriate mating partner, but the sex of an encountered conspecific has to be recognized at a short range as well. Both males and females are able to discriminate between the sexes upon contacting them with their antennae: attracted to a carcass suitable for reproduction, males will fight with males, but tolerate females and vice versa (Pukowski 1933). Moreover, although same sex sexual behavior occasionally occurs (Engel et al. 2015), males usually discriminate between the sexes and copulate with females only. This class level recognition is mediated by contact pheromones on the cuticle: males covered with female cuticular lipids are perceived as females and females covered with male cuticular lipids as males (Steiger et al. 2009). However, although it is known that the composition of the cuticular pattern is sexually dimorphic (*N. vespillpoides*: Steiger et al. 2007; *N. orbicollis*: Scott et al. 2008), the substances responsible for mate discrimination have not been identified yet. As in many invertebrate systems, the mate recognition process is innate, i.e. the beetles have not to learn the cues of a conspecific male or female to be able to discriminate. *N. vespilloides* beetles that had never contact to an adult male or female throughout their life, because they were raised in the absence of parents and afterwards kept in isolation, have still the ability to recognize an appropriate mating partner (personal observations).

The Coolidge Effect

If mating entails costs and there is little benefit to re-mating with the same female, selection should favour the evolution of mechanisms that allow males to preferentially mate with novel females (Adler 1978). The Coolidge effect, defined as a decline in the propensity of a male to copulate repeatedly with the same female combined with a heightened sexual interest in novel females (Wilson et al. 1963; Dewsbury 1981), is expected to be a widespread phenomenon among animals. Although the Coolidge effect has been documented in several vertebrates (mammals: e.g. Rodriguez-Manzo 1999; birds: e.g. Pizzari et al. 2003; reptiles: e.g. Tokarz 1992; amphibians: Donovan and Verrell 1991; e.g. fishes: e.g. Kelley et al. 1999), surprisingly few cases are known in invertebrates (e.g. in the red flour beetle *Tribolium castaneum*: Arnaud and Haubruge 1999; in the pond snail *Lymnaea stagnalis*: Koene and Ter Maat 2007; but not e.g. in the decorated cricket *Gryllodes sigillatus:* Gershman and Sakaluk 2009; or the freshwater snail *Biomphalaria glabrata*: Häderer et al. 2009). One possible explanation for its rareness in invertebrates might be that the Coolidge effect requires an individual's ability to distinguish between its previous partner and a novel mate. However, a study of Steiger et al. (2008a) has demonstrated that burying beetles have this ability and males show greater sexual interest for novel females, irrespective whether these females are virgin or had already mated with other males. There are at least three good reasons, why male burying beetles have evolved the ability to discriminate against a previous mate. First, there is evidence that the supply of sperm in males is not limitless and that frequent mating can leave males sperm-depleted (Eggert 1990). Hence, males should invest their sperm strategically (Wedell et al. 2002). Second, the carcass as valuable resource for feeding and reproduction promotes a temporal clumping of beetles and therefore, there is a risk of remating the same female. Third, there are situations in which copulation with a particular female involves costs in terms of lost opportunities to copulate with other females. Frequently, several females are attracted to a carcass, but most of these potential mates are available for a limited time only, as same sex individuals usually engage in violent fights until only one of them remains in a central position of the carcass (Pukowski 1933; Müller et al. 1990; Eggert and Müller 1997; Scott 1998). Defeated females either leave the carcass immediately for the search of a new one, or stay near the carcass and may succeed in producing some offspring as intraspecific brood parasites (Müller et al. 1990, 2007; Scott and Williams 1993). Therefore, a male investing time by copulating repeatedly with the same female will miss the opportunity to sire some additional offspring with subordinate females that are ultimately expelled from the carcass.

But how do burying beetle males discriminate between their previous mating partner and a novel one? The possibly simplest mechanism that does not require any cognitive abilities, would be to chemically mark the mate during copulation and utilize chemosensory self-referencing to recognize recent mates. There would be no need for learning, rather they could directly compare their own scent with that of the individual with whom they interact (on-line processing sensu Hauber and Sherman 2001). Indeed, this mechanism has been shown in the cricket *G. sigillatus.* In this species, it is the female that discriminates against a previous mate (Ivy et al. 2005). Weddle et al. (2013) has shown that females imbue males with their own unique cuticular hydrocarbon signatures during mating and identify their previous mate based on these cues. However, burying beetles do not appear to transfer any cuticular lipids during mating to mark females. Instead, experiments have shown that they learn their mates' individual specific cuticular pattern during mating: when a male encounters a novel female that is experimentally treated with the same cuticular substances as his previous mate, he mistakes the novel female to be a familiar mate (Steiger et al. 2008a). Although this mechanism is no true individual recognition sensu Gherardi et al. (2012) but an example for familiar recognition, it is still quite sophisticated. First, the chemical cues of females have to be more or less individual-specific, otherwise a male would not be able to discriminate between two random females out of a population, but would make many mistakes. Second, a male must be capable to perceive and learn these individual specific chemical patterns. The composition of the burying beetle's cuticle is highly complex comprising about 100 substances and shows considerable inter-individual variation in their relative proportion (Steiger et al. 2007, 2008a; Engel et al. 2015). The variation of female patterns is even higher than that of males (Steiger et al. 2008a). However, it is currently unknown which of the substances a male can perceive and how many substances he is learning. It would be interesting to see how accurate this recognition system is and how often novel females are confused with previous ones within a population.

Recognition Mechanisms Between Breeding Partners

Even buried carcasses have to be defended by the adult beetles as the corpses can still be discovered by competitors. Successful intruders kill and eat the residents' brood and use the resource for their own reproduction (Robertson 1993; Trumbo 1990c; Trumbo and Valletta 2007; Scott 1990). Infanticide can occur with both, hetero- or conspecifics, and by both, male and female intruders (Scott 1994; Koulianos and Schwarz 2000; Trumbo 1994). When resident beetles encounter intruders, violent fights ensue and males and females assist their mate to drive off intruders of either sex (Scott 1990; Trumbo and Wilson 1993; Trumbo 1991). Hence, individuals rearing a brood on a buried carcass are able to discriminate between their breeding partner and intruding conspecifics (Trumbo and Wilson 1993). However, the beetles do not recognize their individual partners, but their breeding status, i.e. the fact that they have been on a carcass caring for larvae: familiar and unfamiliar brood caring individuals of the opposite sex are generally accepted as nest-mates, whereas non-breeding beetles are attacked (Müller et al. 2003; Fig. 12.1a). Individual recognition is not necessary to defend the offspring, as beetles that are caring for young do not kill larvae of other conspecifics (Müller and Eggert 1990) and are therefore no thread to the brood. Moreover, on larger vertebrate carcasses joint breeding of several males and/or females can be observed (Müller et al. 2007; Scott et al. 2007; Eggert and Müller 1992; Trumbo 1992). Therefore, class-level recognition might be favoured, as learning the individual signature of more than one breeding partner is likely to be a more complicated mechanism than simply to recognize the breeding status of a encountered beetle. Behavioural assays in *N. orbicollis* and *N. vespilloides* have shown that the beetles use chemical recognition cues to discriminate between breeding and non-breeding beetles (Scott et al. 2008; Steiger et al. 2007, 2009). They accept dead breeding beetles and non-breeding beetles that are covered with the chemical cues, i.e. the whole body extract, of breeding beetles. Previous experiments could already exclude the possibility that the cues are merely acquired through contact with or ingestion of carrion (Müller et al. 2003). Chemical analysis via gas chromatography coupled with mass spectrometry revealed that the composition of the cuticular pattern changes within a breeding cycle (Scott et al. 2008; Steiger et al. 2007), and breeding *N. vespilloides* males and females are characterized by a higher proportion of polyunsaturated hydrocarbons, i.e. hydrocarbons with several double bonds, than non-breeding beetles (Steiger et al. 2007, 2008b). In addition, headspace analyses (a technique to elucidate the odour compounds present in the air surrounding an object) brought to light that at least breeding females emit high amount of (*E*)-methyl geranate, a terpenoid, that cannot be detected in females not caring for larvae (Haberer et al. 2010). Behavioural experiments strongly suggest that males rely on both, (*E*)-methyl geranate and cuticular lipids to identify a female's breeding state (Haberer et al. 2010; Steiger et al. 2011b). Interestingly, (*E*)-methyl geranate is structural quite similar to juvenile hormone III (JH III), it only lacks the epoxidised isoprenoid group of JH III. Both molecules most

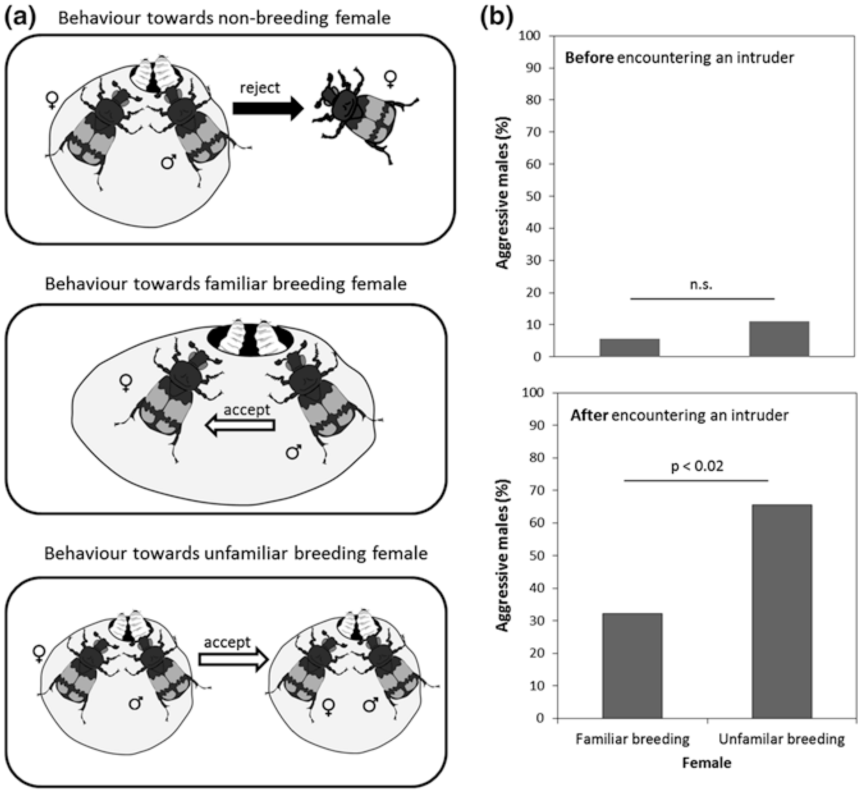


Fig. 12.1 Breeding partner recognition system of the burying beetle *N. vespilloides*. **a** Simplified scheme of the partner recognition system. Breeding males (1) behave aggressively towards non-breeding intruding females, (2) tolerantly towards their own breeding partner, and (3) tolerantly towards unfamiliar breeding females. *Note* it also works for females as receiver and males as sender of the recognition cues. **b** Shift in acceptance threshold. (1) Before encountering an intruding female, breeding males accept both, a familiar and an unfamiliar breeding female and do not discriminate between them. (2) After encountering a female intruder, breeding males become more aggressive towards an unfamiliar than towards a familiar breeding female (Fisher's exact test). *Note* the original experiment was performed with elytra of females, instead of entire females. n.s. = not significant. Modified after Steiger and Müller 2010

likely share the same biosynthetic pathway, the mevalonate pathway (Bellés et al. 2005). In the course of a breeding attempt, females undergo major physiological changes which include an increase in JHIII (Scott et al. 2001; Trumbo et al. 1995; Trumbo 1997; Scott and Panaitof 2004). Therefore, caring females are characterized by very high hormone titres in contrast to non-caring females and they might signal their hormone titre by emitting (*E*)-methyl geranate to make them distinguishable from non-breeding, intruding females (Haberer et al. 2010). Indeed, an additional study revealed that (*E*)-methyl geranate is a signal that has been selected by the effect it has on the receiver and is not simply an unintentional metoabolicby-product of JH synthesis (Steiger et al. 2011b; see also Steiger et al. 2011c for definitions of chemcial cues an signals). Female burying beetles can reproduce alone successfully, they do not necessarily need a male partner to bury a carcass and raise their young (Müller et al. 1998; Scott 1989). Uniparental care occurs regularly in the field (Müller et al. 2007). However, as there is no male partner (i.e. a receiver) in such uniparental situations, there is no need to signal the breeding state to make oneself distinguishable from intruders. In fact, single breeding females have been shown to produce only trace amounts of (*E*)-methyl geranate, 200 times less than paired females (Steiger et al. 2011b).

The chemical composition of the cuticular profile of both, males and females, changes with breeding status, and both, breeding males and females are discriminated from intruders by their partners. The question remains, however, why only breeding females, but not males emit (*E*)-methyl geranate. A proximate reason might be that males have a much lower JH titre (Panaitof et al. 2004) and are therefore not able to produce high amounts of (*E*)-methyl geranate. On an ultimate level, there are at least two non-exclusive explanations. Firstly, the chemical signal has an additional, but hitherto unknown function. Secondly, the task specialization of the sexes is responsible for the differences in chemical signaling. Male burying beetles have a greater tendency and greater ability to guard the brood against conspecific intruders, whereas females spend more time feeding the young (Trumbo 2006). This may lead to a slightly biased signaling system, where females have to be better recognizable and transmit more information than males.

Plasticity of the Partner Recognition System

In nature the cues of desirable and undesirable individuals often overlap. Depending where a receiver individual sets its acceptance threshold, it either runs the risk to make an acceptance or a rejection error. Theoretical models have shown that the optimal acceptance threshold depends on the relative benefits of accepting and rejecting desirable and undesirable senders, the costs of making acceptance and rejection errors and the frequency or future predictability of desirable or undesirable senders (Liebert and Starks 2004; Sherman et al. 1997; Reeve 1989; Davies et al. 1996). An acceptance threshold can be fixed within an individual, however, in more elaborate recognition systems, it may be flexible adjusted to the current situation (e.g. Hauber et al. 2006). In fact, in *N. vespilloides* it has been shown that the acceptance threshold of the breeding partner recognition system changes with the risk of losing the brood due to an infanticidal intruder (Steiger and Müller 2010). As outlined above, the beetles typically discriminate between their breeding partners and conspecific intruders based on a class-specific discrimination rule and do not discriminate between their own and unfamiliar breeding individuals, but are only aggressive towards non-breeding beetles (Fig. 12.1b). After they have encountered an intruder, however, rejection rate increases, which is manifested as a shift from class-specific to a more or less individual-specific discrimination: beetles suddenly begin discriminating between their own breeding partner and an unfamiliar breeding individual, and are more aggressive towards the latter (Steiger and Müller 2010; Fig. 12.1b). The experiments highly suggests that breeding beetles learn the individual specific chemical cues of their own breeding partners and use it as a template, but set their acceptance threshold depending on the risk of encountering an intruder. When the risk is low, the acceptance threshold is more permissive and they also accept conspecifics with cues that are less similar to their template (i.e. unfamiliar breeding beetles). When the risk is high, the acceptance threshold is more restrictive and they only accept conspecifics with cues that are identical or almost identical to their template (i.e. own partner) (Steiger and Müller 2010).

Recognition of the Breeding Partner's Fertility

Although burying beetle males prefer to mate with novel females, they nevertheless mate repeatedly with their breeding partner. In fact, video observations revealed that they mate on average 170 times during a breeding attempt, which lasts about 10 days in *N. vespilloides* (Engel et al. 2014). However mating rate is not constant; it is high in the beginning, but it drops at the time the larvae arrive at the carcass and no mating occurs, when young larvae are present. The copulation pattern corresponds to the oviposition pattern of the females. They lay their eggs in the beginning of the reproductive event over a period of about two days, but during the time of larval feeding, they do not engage in egg laying (Müller 1987). Only if the brood is lost to predators or competitors, females will resume egg-laying (Müller 1987). If females are manipulated experimentally into producing such replacement clutches, males do not cease to mate, but continue to engage in frequent copulations (Engel et al. 2014). Further experiments brought to light, that males do not use the presence or absence of larvae as a cue to adjust copulation rate, but instead use female-produced cues/signals and are able to recognize a female's period of fertility or temporarily infertility (Engel et al. 2014). During parental care, females might either reduce the emission of a substance that otherwise triggers male mating behavior (sex pheromone/aphrodisiac), or they might increase production of a new substance that repels males (antiaphrodisiac). Further experiments are necessary to unravel the exact mechanisms of this recognition process.

Recognition Mechanisms Between Parent and Offspring

The Parents' Viewpoint

When two females compete for a small carcass the defeated females usually do not leave immediately, but lay eggs close to the carcass. This situation has been described as intraspecific brood parasitism, because (1) subordinate females typically abandon the carcass prior to the appearance of larvae and do not provide parental care and (2) the reproduction of subordinate females reduces the dominant's reproductive success (Müller et al. 1990). Subordinate females frequently have some surviving offspring, the composition of the brood, however, is severely skewed in favor of the dominant female. Lab as well as field studies have shown that the brood contains on average 6 % parasite offspring, often not more than one to two young (Müller et al. 1990, 2007). Although the reproductive skew can partly be explained by the loser's inability to produce as many eggs as the winner because of limited access to the carcass and therefore nutrition (Eggert et al. 2008), two different mechanisms of parent-offspring recognition has been found to contribute to the lower reproductive success of the subordinate female. In *N. tomentosus* (Scott 1997), but not in *N. vespilloides* (Eggert et al. 2008), there is some evidence that females increase the proportion of own offspring in a brood by selective ovicide. Although it is not known how they are able to discriminate between their own eggs and the foreign ones, it is possible that individual specific cuticular lipids or other chemicals left behind on the egg surface serve as recognition cues (see e.g. Endler et al. 2004). In *N. orbicollis*, intruders into the brood chambers are also known to destroy eggs of the resident pair before starting their own reproductive attempt (Robertson 1993). However, this is a different situation, as they have not to distinguish their own eggs from the residents' one. Nevertheless, it illustrates that the beetles are able to recognize conspecific eggs and are selected to exhibit oophagy.

The second known mechanism of parent-offspring recognition in burying beetle is a time-dependent recognition mechanism. In general, parental beetles are unable to directly distinguish their own larvae from unrelated conspecific larvae. Dominant females, however, are known to kill all larvae they encounter prior to hatching of their own larvae (Müller and Eggert 1990; Eggert and Müller 2011). Females switch from infanticidal to parental behaviour at about the time their own larvae hatch, and subsequently, they accept newly hatched *Nicrophorus* larvae indiscriminately (Müller and Eggert 1990; Trumbo 1994; Oldekop et al. 2007). Once females have begun to care for larvae, they remain 'parental' until the larvae have completed development on the carcass (Müller and Eggert 1990). That individuals rely on temporal cues as indirect indicators of relatedness to distinguish between their own and unrelated young is not *Nicrophorus*-specific, but is also known from a range of other organisms (Elwood 1994). In burying beetle, such time-dependent recognition mechanism is quite effective in destroying brood-parasitic young: dominant females have been shown to kill over half of the subordinate's larvae by using temporal cues (Eggert and Müller 2011). Certainly, the prerequisite of this mechanism is that some of the subordinate's larvae hatch earlier than that of the dominant one. But exactly this is the case in *N. vespilloides*. Subordinate females have shown to start oviposition nearly one day earlier than dominant ones (Eggert and Müller 2011). The reason for this oviposition pattern is unknown. Both, dominant and subordinate would benefit from late oviposition, as the dominant would improve discrimination between own and foreign young and the subordinate would save its young. However, it is possible that subordinates are constrained to oviposit earlier because of nutritional limitations or injury risk (Eggert and Müller 2011). Interestingly, the temporal recognition mechanism is plastic, too, and the dominant's acceptance threshold depends on the presence or absence of a subordinate. Females breeding with a parasite remain infanticidal until 4 h after their own larvae begin to hatch, whereas singly breeding females begin accepting larvae already 8 h before their own offspring hatch (Eggert and Müller 2011). Though dominant females risk destroying some of their own young by shifting the switch from infanticidal to parental care to a later time, they may be able to kill a greater proportion of the unrelated larvae. Killing own larvae may be less costly than accepting subordinate ones, as female are anyway known to produce surplus hatchlings on small carcasses (Bartlett 1987; Trumbo 1990b).

Both parents are known to react towards a begging larva by providing food (Pukowski 1933). There is evidence that larval begging reflects hunger level, as larvae have been observed to increase their begging behavior following food deprivation (Smiseth and Moore 2004, 2007). Parental resource distribution, in turn, is biased towards food deprived larvae, most certainly because hungry larvae spend more time begging (Smiseth and Moore 2002, 2008). As larvae touch the parent's mouthpart, mechanical cues are likely to play a role in stimulating parental feeding behaviour. However, it cannot be excluded that chemical cues are likewise important. In the earwig *Forficula auraria* (Mas et al. 2009) and the bumblebee *Bombus terrestris* (Den Boer and Duchateau 2006), for example, chemical cues of offspring contain information about nutritional condition and influence the mother's food allocation pattern. In both cases, cuticular lipids appear to be involved. In burying beetles it has never been investigated, whether chemical cues mediate parents' resource distribution within a brood, but there is evidence that chemical cues must be important for offspring recognition. Although, burying beetles are not known to reject heterospecific larvae of the same genus or the sister genus *Ptomascopus* (Trumbo 1994; Trumbo et al. 2001), there at least able to discriminate between burying beetles larvae and *Tenebrio* larvae or dipteran larvae, even there are deposited into the cavity of the carcass together with their own offspring. They selectively fight (*Tenebrio* larvae) or kill and consume (dipteran larvae) them upon contacting them with their antennae (personal observation). Unfortunately, no study has looked into this topic in more detail.

The Offspring's Viewpoint

Larvae do not beg randomly, but increase begging level when a parent is around. Hence, larvae must somehow be able to perceive the presence of a parent or at least a beetle. Although the stridulatory sound parents produce may help to orientate towards a parent (Huerta et al. 1992), it has been shown that acoustic and also behavioral cues are not necessary for triggering begging behavior, as larvae also beg towards a dead beetle (Smiseth and Parker 2008). However, if the parents' cuticular lipids are removed by washing them in pentane, begging behavior is significantly reduced (Smiseth et al. 2010). Thus, chemical stimuli from parents play an important role in parent-offspring interactions. Parents cannot discriminate between related and unrelated offspring based on direct cues about kinship and also offspring appear to lack the ability to distinguish between related and unrelated caretakers, at least they do not show any differences in the time of begging towards their biological mother and an unrelated breeding beetle (Smiseth et al. 2010). However, whereas the parents would benefit if they could discriminate against unrelated larvae based on direct kin recognition cues, the offspring would have no obvious advantage from kin discrimination. In contrast, as a larva might originate from a brood parasite, not displaying any begging behavior towards an unrelated caretaker would reduce its growth and therefore be detrimental. Interestingly, Smiseth et al. (2010) has shown that larvae are able to discriminate between a breeding and a non-breeding and therefore infanticidal female. However, the larvae do not actively avoid non-breeding female intruder, rather they only spend less time begging in the presence of an intruder female. Therefore it is likely that this discrimination is not an adaptive mechanism for avoiding contact with infanticidal females, but is a by-product of stimulus discrimination (Smiseth et al. 2010). As already outlined above, breeding beetles have a different chemical profile than non-breeding ones and as a result chemical cues that trigger begging might be expressed differently in breeding and non-breeding beetles.

Concluding Remarks

In this chapter, I provided an overview of the sophisticated social recognition mechanisms burying beetles have evolved. They are able to recognize the sex of a conspecific, their previous mating partner, their breeding partner, the breeding female's readiness or unreadiness to lay eggs and—by using temporal cues—their offspring. Their discrimination decisions are not static, but can be flexibly adjusted to the current situation. Recognition abilities differ between the sexes. Whereas males are better in defending the brood against conspecific intruders, females are inevitably superior in recognizing offspring, as they have exclusive knowledge about the time of egg laying and therefore larval hatching. Two of the burying beetles' key characteristics, their extended biparental care and reproduction on a small carcass (a valuable and scarce resource), have profoundly influenced the evolution of their recognition system. Biparental care promotes the temporal overlap of individuals for whom mutual recognition is beneficial—breeding partners and their offspring. At the same time, the scarcity of resources essential to reproduction means that breeding beetles will often encounter competitors that are a threat to their own brood—infanticidal intruders, brood parasites and unrelated offspring; recognition of these individuals is also favored. Consequently, neither universal rejection nor universal acceptance of all encountered individuals is an optimal strategy, but discrimination was and is selectively favored in burying beetles.

Acknowledgments I am very thankful to Johannes Stökl and Josef K. Müller for valuable comments on the manuscript. S.S. was supported by a DFG grant (STE 1874/3-1).

References

Adler NT (1978) On the mechanisms of sexual behavior and their evolutionary constraints. In: Hutchinson JB (ed) Biological determinants of sexual behavior. Wiley, New York, pp 655–695

Arce AN, Johnston PR, Smiseth PT, Rozen DE (2012) Mechanisms and fitness effects of antibacterial defences in a carrion beetle. J Evol Biol 25(5):930–937. doi:10.1111/j.1420-9101.2012.02486.x

Arnaud L, Haubruge E (1999) Mating behaviour and male mate choice in *Tribolium castaneum* (Coleoptera, Tenebrionidae). Behaviour 136(1):67–78

Bartlett J (1987) Filial cannibalism in burying beetles. Behav Ecol Sociobiol 21(3):179–183. doi:10.1007/bf00303208

Bartlett J (1988) Male mating success and paternal care in *Nicrophorus vespilloides* (Coleoptera: Silphidae). Behav Ecol Sociobiol 23(5):297–304

Beeler AE, Rauter CM, Moore AJ (1999) Pheromonally mediated mate attraction by males of the burying beetle *Nicrophorus orbicollis*: alternative calling tactics conditional on both intrinsic and extrinsic factors. Behav Ecol 10(5):578–584

Beeler AE, Rauter CM, Moore AJ (2002) Mate discrimination by females in the burying beetle *Nicrophorus orbicollis*: the influence of male size on attractiveness to females. Ecol Entomol 27(1):1–6

Bellés X, Martin D, Piulachs MD (2005) The mevalonate pathway and the synthesis of juvenile hormone in insects. Annu Rev Entomol 50:181–199

Cotter SC, Kilner RM (2009) Sexual division of antibacterial resource defence in breeding burying beetles *Nicrophorus vespilloides*. J Anim Ecol. doi:10.1111/j.1365-2656.2009.01593.x

Cotter SC, Topham E, Price AJP, Kilner RM (2010) Fitness costs associated with mounting a social immune response. Ecol Lett 13(9):1114–1123. doi:10.1111/j.1461-0248.2010.01500.x

Davies NB, Brooke MDL, Kacelnik A (1996) Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. Proc R Soc B—Biol Sci 263(1372):925–931

Den Boer SPA, Duchateau M (2006) A larval hunger signal in the bumblebee *Bombus terrestris*. Insectes Soc 53(3):369–373

Dewsbury DA (1981) Effects of novelty on copulatory-behavior—the coolidge effect and related phenomena. Psychol Bull 89(3):464–482

Donovan A, Verrell PA (1991) The effect of partner familiarity on courtship success in the salamander *Desmognathus ochrophaeus*. J Herpetol 25(1):93–95

Eggert AK (1990) Chemische Kommunikation beim Totengräber *Necrophorus vespilloides* Herbst (Coleoptera: Silphidae): Pheromonabgabe als alternative Fortpflanzungstaktik der Männchen. Ph.D. thesis, University of Bielefeld, Bielefeld, Germany

Eggert AK, Müller JK (1989a) Mating success of pheromone-emitting *Necrophorus* males: do attracted females discriminate against resource owners? Behaviour 110(1–4):248–257

Eggert AK, Müller JK (1989b) Pheromone-mediated attraction in burying beetles. Ecol Entomol 14(2):235–238

Eggert A-K, Müller JK (1992) Joint breeding in female burying beetles. Behav Ecol Sociobiol 31(4):237–242

Eggert A-K, Müller JK (1997) Biparental care and social evolution in burying beetles: lessons from the larder. In: Choe JC, Crespi BJ (eds) The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge, New York, pp 216–236

Eggert A-K, Müller JK (2011) Timing of oviposition enables dominant female burying beetles to destroy brood-parasitic young. Animal Behaviour 82(6):1227–1233. doi:10.1016/j.anbehav.2011.09.001

Eggert AK, Otte T, Müller JK (2008) Starving the competition: a proximate cause of reproductive skew in burying beetles (*Nicrophorus vespilloides*). Proc R Soc B 275(1650):2521–2528. doi:10.1098/rspb.2008.0661

Elwood RW (1994) Temporal-based kinship recognition: a switch in time saves mine. Behav Process 33:15–24. doi:10.1016/0376-6357(94)90057-4

Endler A, Liebig J, Schmitt T, Parker JE, Jones GR, Schreier P, Hölldobler B (2004) Surface hydrocarbons of queen eggs regulate worker reproduction in a social insect. Proc Natl Acad Sci USA 101(9):2945–2950

Engel KC, von Hoermann C, Eggert A-K, Müller JK, Steiger S (2014) When males stop having sex: adaptive insect mating tactics during parental care. Anim Behav 90(0):245–253. doi:10.1016/j.anbehav.2014.02.006

Engel K, Männer L, Ayasse M, Steiger S (2015) Acceptance threshold theory can explain occurrence of homosexual behaviour. Biol Lett 11:20140603 10.1098/rsbl.2014.0603

Fabre JH (1899) Souvenirs Entomologiques, vol 6. Paris

Fetherston IA, Scott MP, Traniello JFA (1990) Parental care in burying beetles: the organization of male and female brood-care behavior. Ethology 85(3):177–190. doi:10.1111/j.1439-0310.1990.tb00398.x

Gershman SN, Sakaluk SK (2009) No coolidge effect in decorated crickets. Ethology 115(8):774–780. doi:10.1111/j.1439-0310.2009.01663.x

Gherardi F, Aquiloni L, Tricarico E (2012) Revisiting social recognition systems in invertebrates. Animal cognition 15(5):745–762

Haberer W, Schmitt T, Peschke K, Schreier P, Müller JK (2008) Ethyl 4-methyl heptanoate: a male-produced pheromone of *Nicrophorus vespilloides*. J Chem Ecol 34(1):94–98

Haberer W, Steiger S, Müller JK (2010) (*E*)-Methylgeranate, a chemical signal of juvenile hormone titre and its role in the partner recognition system of burying beetles. Anim Behav 79(1):17–24. doi:10.1016/j.anbehav.2009.09.019

Haberer W, Schmitt T, Schreier P, Muller JK (2011) Intended and unintended receivers of the male pheromones of the burying beetles *Nicrophorus humator* and *Nicrophorus vespilloides*. Entomol Exp Appl 140(2):122–126. doi:10.1111/j.1570-7458.2011.01143.x

Häderer IK, Werminghausen J, Michiels NK, Timmermeyer N, Anthes N (2009) No effect of mate novelty on sexual motivation in the freshwater snail *Biomphalaria glabrata*. Front Zool 6:23

Hall CL, Wadsworth NK, Howard DR, Jennings EM, Farrell LD, Magnuson TS, Smith RJ (2011) Inhibition of microorganisms on a carrion breeding resource: the antimicrobial peptide activity of burying beetle (Coleoptera: Silphidae) oral and anal secretions. Environ Entomol 40(3):669–678

Hauber ME, Sherman PW (2001) Self-referent phenotype matching: theoretical considerations and empirical evidence. Trends Neurosci 24(10):609–616

Hauber ME, Moskat C, Ban M (2006) Experimental shift in hosts' acceptance threshold of inaccurate-mimic brood parasite eggs. Biol Lett 2(2):177–180. doi:10.1098/rsbl.2005.0438

Huerta C, Halffter G, Fresneau D (1992) Inhibition of stridulation in *Nicrophorus* (Coleoptera: Silphidae): consequences for reproduction. Elytron 6:151–157

Ivy TM, Weddle CB, Sakaluk SK (2005) Females use self-referent cues to avoid mating with previous mates. Proc R Soc B 272(1580):2475–2478

Kelley JL, Graves JA, Magurran AE (1999) Familiarity breeds contempt in guppies. Nature 401(6754):661–662

Kilner RM, Langmore NE (2011) Cuckoos versus hosts in insects and birds: adaptations, counter-adaptations and outcomes. Biol Rev 86(4):836–852. doi:10.1111/j.1469-185X.2010.00173.x

Koene JM, Ter Maat A (2007) Coolidge effect in pond snails: male motivation in a simultaneous hermaphrodite. BMC Evol Biol 7

Koulianos S, Schwarz HH (2000) Probability of intra- and interspecific encounters, and the duration of parental care in *Nicrophorus investigator* (Coleoptera: Silphidae). Ann Entomol Soc Am 93(4):836–840

Liebert AE, Starks PT (2004) The action component of recognition systems: a focus on the response. Ann Zool Fennici 41(6):747–764

Mas F, Haynes KF, Kölliker M (2009) A chemical signal of offspring quality affects maternal care in a social insect. Proc R Soc B 276(1668):2847–2853. doi:10.1098/rspb.2009.0498

Müller JK (1987) Replacement of a lost clutch—a strategy for optimal resource utilization in *Necrophorus vespilloides* (Coleoptera, Silphidae). Ethology 76(1):74–80

Müller JK, Eggert A-K (1987) Effects of carrion-independent pheromone emission by male burying beetles (Silphidae: *Necrophorus*). Ethology 76:297–304

Müller JK, Eggert AK (1990) Time-dependent shifts between infanticidal and parental behavior in female burying beetles a mechanism of indirect mother-offspring recognition. Behav Ecol Sociobiol 27(1):11–16

Müller JK, Eggert AK, Dressel J (1990) Intraspecific brood parasitism in the burying beetle *Necrophorus vespilloides* Coleoptera Silphidae. Anim Behav 40(3):491–499

Müller JK, Eggert A-K, Sakaluk SK (1998) Carcass maintenance and biparental brood care in burying beetles: are males redundant? Ecol Entomol 23(2):195–200

Müller JK, Eggert A-K, Elsner T (2003) Nestmate recognition in burying beetles: the "breeder's badge" as a cue used by females to distinguish their mates from male intruders. Behav Ecol 14:212–220

Müller JK, Braunisch V, Hwang WB, Eggert AK (2007) Alternative tactics and individual reproductive success in natural associations of the burying beetle, *Nicrophorus vespilloides*. Behav Ecol 18(1):196–203

Niemitz C, Krampe A (1972) Untersuchungen zum Orientierungsverhalten der Larven von *Necrophorus vespillo* F. (Silphidae Coleoptera). Zeitschrift für Tierpsychologie 30(5):456–463

Oldekop JA, Smiseth PT, Piggins HD, Moore AJ (2007) Adaptive switch from infanticide to parental care: how do beetles time their behaviour? J Evol Biol 20(5):1998–2004

Panaitof SC, Scott MP, Borst DW (2004) Plasticity in juvenile hormone in male burying beetles during breeding: physiological consequences of the loss of a mate. J Insect Physiol 50(8):715–724

Peck S, Kaulbars M (1987) A synopsis of the distribution and bionomics of the carrion beetles (Coleoptera: Silphidae) of the conterminous United States. Proc Entomol Soc Ontario 118:47–81

Pizzari T, Cornwallis CK, Lovlie H, Jakobsson S, Birkhead TR (2003) Sophisticated sperm allocation in male fowl. Nature 426(6962):70–74

Pukowski E (1933) Ökologische Untersuchungen an *Necrophorus* F. Z Morphol Ökol Tiere 27:518–586

Rauter CM, Moore AJ (1999) Do honest signalling models of offspring solicitation apply to insects? Proc R Soc Lond B Biol Sci 266(1429):1691–1696. doi:10.1098/rspb.1999.0833

Reeve HK (1989) The evolution of conspecific acceptance thresholds. Am Nat 133(3):407–435

Robertson IC (1993) Nest intrusions, infanticide, and parental care in the burying beetle, *Nicrophorus orbicollis* (Coleoptera: Silphidae). J Zool 231(4):583–593

Rodriguez-Manzo G (1999) Blockade of the establishment of the sexual inhibition resulting from sexual exhaustion by the Coolidge effect. Behav Brain Res 100(1–2):245–254

Royle NJ, Hopwood PE, Head ML (2013) Burying beetles. Curr Biol 23(20):R907–R909. doi:10.1016/j.cub.2013.07.066

Scott MP (1989) Male parental care and reproductive success in the burying beetle *Nicrophorus orbicollis*. J Insect Behav 2(1):133–138

Scott MP (1990) Brood guarding and the evolution of male parental care in burying beetles. Behav Ecol Sociobiol 26(1):31–40

Scott MP (1994) The benefit of paternal assistance in intra- and interspecific competition for the burying beetle *Nicrophorus defodiens*. Ethol Ecol Evol 6(4):537–543

Scott MP (1997) Reproductive dominance and differential ovicide in the communally breeding burying beetle *Nicrophorus tomentosus*. Behav Ecol Sociobiol 40(5):313–320

Scott MP (1998) The ecology and behavior of burying beetles. Annu Rev Entomol 43:595–618

Scott MP, Panaitof SC (2004) Social stimuli affect juvenile hormone during breeding in biparental burying beetles (Silphidae: *Nicrophorus*). Horm Behav 45(3):159–167

Scott MP, Traniello JFA (1990) Behavioral and ecological correlates of male and female parental care and reproductive success in burying beetles *Nicrophorus spp*. Anim Behav 39(2):274–283

Scott MP, Williams SM (1993) Comparative reproductive success of communally breeding burying beetles as assessed by PCR with randomly amplified polymorphic DNA. Proc Natl Acad Sci 90(6):2242–2245

Scott MP, Trumbo ST, Neese PA, Bailey WD, Roe RM (2001) Changes in biosynthesis and degradation of juvenile hormone during breeding by burying beetles: a reproductive or social role? J Insect Physiol 47(3):295–302

Scott MP, Lee WJ, van der Reijden ED (2007) The frequency and fitness consequences of communal breeding in a natural population of burying beetles: a test of reproductive skew. Ecol Entomol 32(6):651–661

Scott MP, Madjid K, Orians CM (2008) Breeding alters cuticular hydrocarbons and mediates partner recognition by burying beetles. Anim Behav 76:507–513

Sherman PW, Reeve HK, Pfennig DW (1997) Recognition systems. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach, 4th edn. Blackwell Science, Oxford, pp 69–96

Sikes DS, Venables C (2013) Molecular phylogeny of the burying beetles (Coleoptera: Silphidae: Nicrophorinae). Mol Phylogenet Evol 69(3):552–565. doi:10.1016/j.ympev.2013.07.022

Smiseth PT, Moore AJ (2002) Does resource availability affect offspring begging and parental provisioning in a partially begging species? Anim Behav 63(3):577–585

Smiseth PT, Moore AJ (2004) Signalling of hunger when offspring forage by both begging and self-feeding. Anim Behav 67:1083–1088. doi:10.1016/j.anbehav.2003.10.012

Smiseth PT, Moore AJ (2007) Signalling of hunger by senior and junior larvae in asynchronous broods of a burying beetle. Anim Behav 74(4):699–705

Smiseth PT, Moore AJ (2008) Parental distribution of resources in relation to larval hunger and size rank in the burying beetle *Nicrophorus vespilloides*. Ethology 114(8):789–796

Smiseth PT, Parker HJ (2008) Is there a cost to larval begging in the burying beetle Nicrophorus vespilloides? Behav Ecol 19(6):1111–1115. doi:10.1093/beheco/arn101

Smiseth PT, Darwell CT, Moore AJ (2003) Partial begging: an empirical model for the early evolution of offspring signalling. Proc R Soc B 270(1526):1773–1777

Smiseth PT, Andrews C, Brown E, Prentice PM (2010) Chemical stimuli from parents trigger larval begging in burying beetles. Behav Ecol 21(3):526–531

Steiger S (2013) Bigger mothers are better mothers: disentangling size-related prenatal and postnatal maternal effects. Proc R Soc B 280:20131225. doi:10.1098/rspb.2013.1225

Steiger S, Müller JK (2010) From class-specific to individual discrimination: acceptance threshold changes with risk in the partner recognition system of the burying beetle *Nicrophorus vespilloides*. Anim Behav 80(4):607–613. doi:10.1016/j.anbehav.2010.06.018

Steiger S, Peschke K, Francke W, Müller JK (2007) The smell of parents: breeding status influences cuticular hydrocarbon pattern in the burying beetle *Nicrophorus vespilloides*. Proc R Soc B 274:2211–2220

Steiger S, Franz R, Eggert A-K, Müller JK (2008a) The Coolidge effect, individual recognition and selection for distinctive cuticular signatures in a burying beetle. Proc R Soc B 275(1645):1831–1838

Steiger S, Peschke K, Müller JK (2008b) Correlated changes in breeding status and polyunsaturated cuticular hydrocarbons: the chemical basis of nestmate recognition in the burying beetle *Nicrophorus vespilloides*? Behav Ecol Sociobiol 62:1053–1060

Steiger S, Whitlow S, Peschke K, Müller JK (2009) Surface chemicals inform about sex and breeding status in the biparental burying beetle *Nicrophorus vespilloides*. Ethology 115(2):178–185

Steiger S, Gershman SN, Pettinger AM, Eggert A-K, Sakaluk SK (2011a) Sex differences in immunity and rapid upregulation of immune defence during parental care in the burying beetle, *Nicrophorus orbicollis*. Funct Ecol 25:1368–1378

Steiger S, Haberer W, Müller JK (2011b) Social environment determines degree of chemical signalling. Biol Lett 7:822–824. doi:10.1098/rsbl.2011.0457

Steiger S, Schmitt T, Schaefer HM (2011c) The origin and dynamic evolution of chemical information transfer. Proc R Soc B 278(1708):970–979. doi:10.1098/rspb.2010.2285

Suzuki S (2001) Suppression of fungal development on carcasses by the burying beetle *Nicrophorus quadripunctatus* (Coleoptera: Silphidae). Entomol Sci 4:403–406

Suzuki S, Nagano M (2009) To compensate or not? Caring parents respond differentially to mate removal and mate handicapping in the burying beetle *Nicrophorus quadripunctatus*. Ethology 115(1):1–6. doi:10.1111/j.1439-0310.2008.01598.x

Tokarz RR (1992) Male mating preference for unfamiliar females in the lizard *Anolis sagrei*. Anim Behav 44(5):843–849

Trumbo ST (1990a) Interference competition among burying beetles (Silphidae, *Nicrophorus*). Ecol Entomol 15(3):347–355

Trumbo ST (1990b) Regulation of brood size in a burying beetle *Nicrophorus tomentosus* Silphidae. J Insect Behav 3(4):491–500

Trumbo ST (1990c) Reproductive benefits of infanticide in a biparental burying beetle *Nicrophorus orbicollis*. Behav Ecol Sociobiol 27(4):269–274

Trumbo ST (1991) Reproductive benefits and the duration of paternal care in a biparental burying beetle *Necrophorus orbicollis*. Behaviour 117(1–2):82–105

Trumbo ST (1992) Monogamy to communal breeding: exploitation of a broad resource base by burying beetles (*Nicrophorus*). Ecol Entomol 17(3):289–298

Trumbo ST (1994) Interspecific competition, brood parasitism, and the evolution of biparental cooperation in burying beetles. Oikos 69(2):241–249

Trumbo ST (1997) Juvenile hormone-mediated reproduction in burying beetles: from behavior to physiology. Arch Insect Biochem Physiol 35(4):479–490

Trumbo ST (2006) Infanticide, sexual selection and task specialization in a biparental burying beetle. Anim Behav 72:1159–1167

Trumbo ST, Robinson GE (2004) Nutrition, hormones and life history in burying beetles. J Insect Physiol 50(5):383–391

Trumbo ST, Valletta RC (2007) The costs of confronting infanticidal intruders in a burying beetle. Ethology 113(4):386–393

Trumbo ST, Wilson DS (1993) Brood discrimination, nest mate discrimination, and determinants of social behavior in facultatively quasisocial beetles (*Nicrophorus* spp.). Behav Ecol 4(4):332–339

Trumbo ST, Borst DW, Robinson GE (1995) Rapid elevation of juvenile hormone titer during behavioral assessment of the breeding resource by the burying beetle *Nicrophorus orbicollis*. J Insect Physiol 41(6):535–543

Trumbo ST, Kon M, Sikes D (2001) The reproductive biology of *Ptomascopus morio*, a brood parasite of Nicrophorus. J Zool 255(4):543–560

Walling CA, Stamper CE, Smiseth PT, Moore AJ (2008) The quantitative genetics of sex differences in parenting. Proc Natl Acad Sci 105(47):18430–18435. doi:10.1073/pnas.0803146105

Weddle CB, Steiger S, Hamaker CG, Ower GD, Mitchell C, Sakaluk SK, Hunt J (2013) Cuticular hydrocarbons as a basis for chemosensory self-referencing in crickets: a potentially universal mechanism facilitating polyandry in insects. Ecol Lett 16(3):346–353. doi:10.1111/ele.12046

Wedell N, Gage MJG, Parker GA (2002) Sperm competition, male prudence and sperm-limited females. Trends Ecol Evol 17(7):313–320

Wilson JR, Kuehn RE, Beach FA (1963) Modification in sexual behavior of male rats produced by changing stimulus female. J Comp Physiol Psychol 56(3):636–644