Current Zoology, 2021, 67(5), 515–518
doi: 10.1093/cz/zoab065
Advance Access Publication Date: 7 August 2021
Editorial

Editorial

Uncovering variation in social insect communication

Alessandro Cini[a,b,*], Luca Pietro Casacci[c,*], and Volker Nehring[d,*]

[a]Centre for Biodiversity & Environment Research, University College London, Gower Street, London, WC1E 6BT, UK, [b]Dipartimento di Biologia, Università degli Studi di Firenze, Via Madonna del Piano, Sesto Fiorentino, Firenze, 50019, Italy, [c]Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, Turin, 10123, Italy, and [d]Department of Evolutionary Biology and Ecology, Institute of Biology I (Zoology), University of Freiburg, Hauptstraße 1, Freiburg (Brsg.), 79104, Germany

*Address correspondence to Alessandro Cini, Luca Pietro Casacci, and Volker Nehring. E-mail: cini.ales@gmail.com, luca.casacci@unito.it, volker.nehring@biologie.uni-freiburg.de

accepted on 5 August 2021

Introduction

Social life within insect societies is regulated by a sophisticated multimodal communication network. Complex blends of chemical compounds are integrated with vibrational, acoustic, and visual signals to control the division of labor in the colony, from colony defense to brood care (d'Ettorre and Moore 2008; Richard and Hunt 2013; Cervo et al. 2015). It is no surprise that the study of communication has historically represented a fruitful area of investigation, leading to marvelous discoveries such as the complexities of the honeybee dance communication (von Frisch 1967; I'Anson Price and Grüter 2015) and the sophisticated multimodal deception strategies adopted by socially parasitic species to exploit their hosts (Lenoir et al 2001; Nash and Boomsma 2008; Barbero et al. 2009; Casacci et al. 2021).

The recent years have brought a new appreciation specifically for the variation in social insect communication (Figure 1A). Not all species behave in the same way as the typical model organisms, such as honeybees, do. Moreover, many examples have been put forward of considerable and often unexpected intraspecific variation that seems like a hindrance for research at first, but can ultimately help us to better understand the evolution of behaviors (Nehring et al. 2013). For example, signal production and response have been shown to dramatically vary geographically, so that the same "message" can be conveyed by different signals in different populations (e.g., geographic variation in nestmate recognition cues in ants, Buczkowski and Silverman 2006; social rank signaling in wasps, Dapporto et al. 2004), or specific signaling systems can be lacking from entire populations (geographic variation in the use of visual cues for social recognition in *Polistes* wasps, Cervo et al. 2015; Tibbetts et al. 2021). Also, signal use might strongly depend on the context (Cini et al. 2019), so that the response to pheromones, for example, depends on the simultaneous presence of other cues/signals or is even affected by individual experience (reviewed in Orlova and Amsalem 2019 and Grüter and Czaczkes 2019).

Such diversity and plasticity are the focus of this special column, which aims at promoting the research effort into variation in social insect communication. We believe that to understand how communication evolves and regulates the fascinating insect societies, a deep and extensive comprehension of the variation in communication, and its causes and consequences, is required. Diversity and plasticity of communication are crucial factors facilitating the evolutionary and ecological success of social insects and their survival in this rapidly changing Anthropocenic era (Chapman and Bourke 2001; Fisher et al. 2019). This special column gathers five research articles that document variation in social insect communication at several levels, from fertility signaling within colonies to information exchange while foraging, using the three groups of social Hymenoptera: ant, bees, and wasps (Figure 1B). The work of more than 20 authors from 8 countries provides an update of some research avenues that go toward the uncovering of variation in social insect communication.

The Contributions to the Special Column

Two contributions deal with intracolonial chemical communication, in particular with the variation in cuticular hydrocarbon (CHC) profiles. CHC profiles consist of complex mixtures of long-chained hydrocarbons such as linear alkanes, alkenes, and mono-, di-, and tri-methyl branched alkanes (Blomquist and Bagnères 2010). The CHCs form a lipid layer that covers each insects' epicuticle, sometimes accompanied by other compounds, such as esters, alcohols, and fatty acids (Lockey 1988). CHCs primarily evolved as an anti-desiccation and protection layer on the insect cuticle, but during the evolution of sociality they have also acquired a crucial role as major

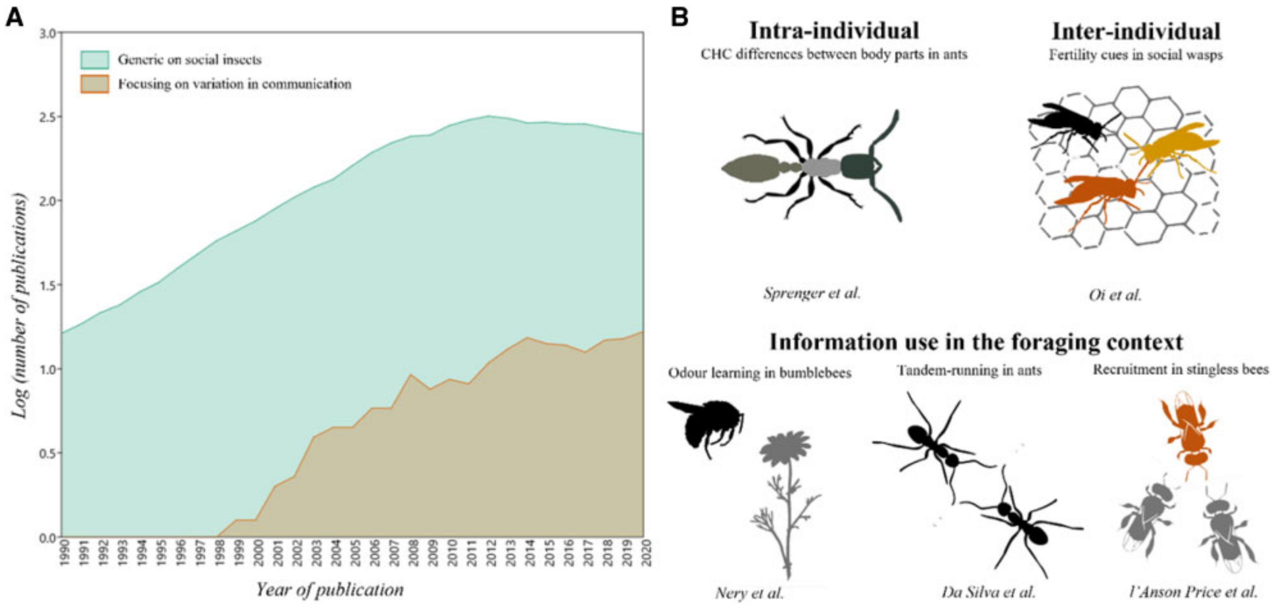

Figure 1. (**A**) The attention toward variation, diversity, and plasticity of social insect communication has increased in the last years, as shown by a literature search on the Scopus database. The graph shows the log number of published papers versus year of publication in the time period 1990–2020. Papers on variation, diversity, or plasticity in social insect communication *(query: TITLE-ABS-KEY("social insect*" AND (communication OR signal* OR pheromon*) AND (variation OR diversity OR plasticity)))* increased more than generic papers on social insects *(query: TITLE-ABS-KEY("social insect*"))*; (**B**) the topics and study organisms of the contributions to this special column (images, modified, from Phylopic.org and Wikimedia commons).

communication molecules (Blomquist and Bagnères 2010; Leonhardt et al. 2016). In social insects, CHCs mediate many forms of recognition and information transfer, such as fertility signaling, nestmate recognition, and foraging recruitment (Sprenger and Menzel 2020). The importance of CHCs in many aspects of social insect communication makes them ideal models to investigate the causes and consequences of variation in complex traits.

A first obvious level of variation in CHCs is interindividual differences among nestmates. Indeed, CHCs strongly vary among individuals within a colony, differing among castes, sexes, and varying according to individual features such as the mating status or health (Sprenger and Menzel 2020). Individual variation in CHC blend composition within a colony also strongly contributes to what could be considered the quintessence of advanced sociality: reproductive division of labor, whereby some individuals specialize in reproduction while others help maintain the nest and provision and defend the brood (Robinson 1992). In advanced eusocial species, such as yellowjackets, chemical communication plays a key role in regulating reproductive division of labor. The queen possesses specific CHCs that prevent worker reproduction, and thereby maintain the queen's reproductive monopoly (Oliveira et al. 2017). How this chemical regulation evolved from solitary ancestors is still debated (Nehring and Steiger 2018). One intriguing hypothesis is that reproduction and fertility-associated chemical cues were physiologically coupled already in solitary ancestors. If both were under the control of a single hormonal factor (hormonal pleiotropy hypothesis, with the ubiquitous insect growth regulator Juvenile Hormone (JH); (Riddiford 2012) as a prime candidate, Flatt et al. 2005; Oi et al. 2015), this predisposition would facilitate the evolution of queen pheromones and maintain signal honesty (Leonhardt et al. 2016).

Oi et al. (2021) tested this hypothesis in four Polistine wasps, whose rather small and flexible societies are suitable models to investigate the evolution of fertility signaling. Using both an analog and an inhibitor of JH, Oi et al. were able to experimentally manipulate the endogenous levels of JH and to analyze the effects on fertility and fertility signaling. Their results provide good support for the hormonal pleiotropy hypothesis, as hormonal treatment influenced both ovarian development (i.e., fertility) and the abundance of fertility-specific CHCs. This provides support to the idea that queen pheromones in eusocial insects might have evolved from chemical variation that was already present, but not used to convey information, in solitary ancestors (Leonhardt et al. 2016).

While CHC variation between individuals has been widely documented (Sprenger and Menzel 2020), the possibility that CHC blends might differ within the same individual has rarely received attention (Bonavita-Cougourdan et al. 1993; Wang et al. 2016; Wang et al. 2019). Sprenger et al. (2021) now provide the first evidence that CHC variation among body parts is far from being an exception in ants. In their paper, the authors investigated the CHC composition of different body parts in 17 ant species from three different genera. They found significant variation in the blend composition, with some body parts being richer in solid CHCs, which melt at higher temperatures, and other parts where liquid CHCs, melting at lower temperatures, were more abundant. Interestingly, this pattern was rather consistent across species, highlighting the relevance of this phenomenon and suggesting a common mechanism for its presence across the studied species. The authors discuss the possible causes, for example, differential rates of transfer and abrasion of CHC classes according to their biophysical properties, or a regionalization in their secretion. Sprenger et al. also evaluate the potential consequences of such intra-individual variation in CHC composition: the intra-individual variation might be a factor promoting the maintenance of intra-colonial variation in CHCs while at the same time maintaining a homogenous colony odor. For example, queen pheromones that only the queen should bear may be displayed on one body part only, while the nestmate recognition cues, which should be uniform across all individuals, are on all other parts of the body. The study has far-reaching consequences for social insect researchers. Often, the analysis of only a part of the body is used as a proxy for the entire animal. Future studies should demonstrate the extent to which such approximation is admissible. The findings also trigger many exciting new research questions: To what extent is intra-individual variation in CHCs present in other social insect taxa, such as wasps and termites? What are the consequences of communication and recognition? Are individuals analyzing the CHCs of different body parts to acquire different information? Surely, these findings strongly support the need to include another level of variation in the study of chemical communication within insect societies.

Social insects are often considered to be successful because their ability to coordinate makes foraging for food very efficient. Once a worker has found a profitable food source, it can directly guide other individuals there, or it can lay pheromone trails to the food source. Honeybees can point other bees in the right direction using their famous waggle dance (von Frisch 1967). However, coordinated foraging represents only part of the foraging behaviors in most species: often, workers forage alone. In this special column, we particularly appreciate the variation in communication by covering non-model social insects, ecological effects, and interspecific variation.

Nery et al. (2021) were the first to study appetitive learning in the bumblebee *Bombus pauloensis*. This species is understudied in comparison to other bumblebees like *B. terrestris*, despite its commercial significance as a pollinator. Nery et al. show that a standardized conditioning protocol developed in honeybees, which is based on observing the proboscis extension reflex in harnessed individuals that cannot fly, is also successful in this species. The bumblebees could remember food-associated odors for at least 48 h. In addition, Nery et al. show that the bumblebees could transfer what they learned in the highly controlled setup to more natural contexts when they could freely fly in cages. The proboscis extension reflex is thus both a feasible and a meaningful method when working with *B. pauloensis*.

The work conducted by da Silva et al. (2021) highlights how social insects can be flexible in their collective and individual foraging behavior in response to the immediate context and information on the food source. The authors evaluated how workers of the ant species *Pachycondyla striata* can select different foraging strategies, that is, forage solitarily, or recruit and lead nestmates to the food through tandem running, when food sources vary by their nature (proteins vs. carbohydrates), size, and distance from the nest, at different temperatures and humidity. Their results show that tandem runs are quite common, and most ants use this strategy regularly. However, the tandem running frequency was greater when resources were closer to the nest and the relative humidity was higher. Interestingly, tandem runs involving food sources at greater distances were more successful when food sources consisted of proteins, suggesting that a more complex transfer of information takes place between leader and follower ants than previously thought, and that possibly experience and motivation of individuals also play a role.

Besides the enormous amount of data collected, this study provides a valuable contribution to the study of recruitment and foraging in the ant subfamily Ponerinae, which is little studied compared to other species of tandem runners, for example, *Temnothorax* sp., and to those ant species characterized by mass recruitment. Compared to other studies that were conducted almost exclusively under laboratory conditions, the study by da Silva et al. shows how the studied insects behave in their natural habitat. The results are therefore realistic and reinforce the knowledge gained from previous laboratory studies, laying the foundations for new field studies on foraging.

Even though recruiting nestmates to food sources, for example, through tandem runs, seems intuitively advantageous, only few tests of this claim exist (e.g. Seeley 1983). I'Anson Price et al. (2021) set out to test whether species with mass recruitment indeed forage more efficiently than species without mass recruitment, using a set of 13 sympatric Brazilian stingless bee species. Surprisingly, they found no evidence for recruiting species collecting higher-quality food, or more food, in a given time, than species whose workers forage on their own. This curious finding begs the question how else the relatively elaborate communication that supports mass-recruiting can pay off, if not through quality or quantity of food. The authors speculate that mass-recruiting may allow species to monopolize certain food sources and thus provide the colonies with a constant food supply, which may have beneficial effects only in the long run or under certain conditions.

Perspective

The studies compiled in this special column all have the same important message: we need to be aware of potential variation in the traits that we study. Ignoring variation can lead to false conclusions when transferring knowledge from one part of the world to another—heads do not smell like feet. Similarly, if different studies find different traits for different species, this does not necessarily mean that the species always differ: if behavior is measured in one context in one species, but in another context in another species, functional and dynamic intraspecific variation may be mistaken for a static interspecific difference. Finally, hypotheses on the evolution of variation deserve rigorous testing. While it may be easy to devise intuitive explanations for why two species differ in their communication, the actual fitness effects may be surprisingly weak.

Acknowledgments

We would like to thank all the authors that contributed to this special column, as well as all those that dedicated their time and expertise as reviewers.

Conflict of Interest Statement

The authors declare no conflict of interest.

References

Barbero F, Thomas JA, Bonelli S, Balletto E, Schönrogge K, 2009. Queen ants make distinctive sounds that are mimicked by a butterfly social parasite. *Science* **323**: 782–785.

Blomquist GJ, Bagnères AG, 2010. Introduction: history and overview of insect hydrocarbons. In: Blomquist GJ, Bagnères AG, editors. *Insect Hydrocarbons: Biology, Biochemistry, and Chemical Ecology*. New York: Cambridge University Press. 3–18.

Bonavita-Cougourdan A, Clement J-L, Lange C, 1993. Functional subcaste discrimination (foragers and brood-tenders) in the ant *Camponotus vagus* Scop.: polymorphism of cuticular hydrocarbon patterns. *J Chem Ecol* **19**: 1461–1477.

Buczkowski G, Silverman J, 2006. Geographical variation in Argentine ant aggression behaviour mediated by environmentally derived nestmate recognition cues. *Anim Behav* **71**:327–335.

Casacci LP, Barbero F, Ślipiński P, Witek M, 2021. The inquiline ant *Myrmica karavajevi* uses both chemical and vibroacoustic deception mechanisms to integrate into its host colonies. *Biology* **10**:654.

Cervo R, Cini A, Turillazzi S, 2015. Visual recognition in social wasps. In: Aquiloni L, Tricarico E, editors. *Social Recognition in Invertebrates*. Cham: Springer. 125–145.

Chapman RE, Bourke AF, 2001. The influence of sociality on the conservation biology of social insects. *Ecol Lett* **4**:650–662.

Cini A, Cappa F, Pepiciello I, Platania L, Dapporto L et al., 2019. Sight in a clique, scent in society: plasticity in the use of nestmate recognition cues along colony development in the social wasp *Polistes dominula*. *Front Ecol Evol* **7**: 444.

d'Ettorre P, Moore AJ, 2008. Chemical communication and the coordination of social interactions in insects. In: d'Ettorre P, Hughes DP, editors. *Sociobiology of Communication: An Interdisciplinary Perspective*. Oxford: Oxford University Press. 81–96.

da Silva JP, Valadares L, de Lima Vieira ME, Teseo S, Châline N, 2021. Tandem running by foraging *Pachycondyla striata* workers in field conditions vary in response to food type, food distance, and environmental conditions. *Curr Zool* **67**:541–549.

Dapporto L, Theodora P, Spacchini C, Pieraccini G, Turillazzi S, 2004. Rank and epicuticular hydrocarbons in different populations of the paper wasp *Polistes dominulus* (Christ) (Hymenoptera, Vespidae). *Insectes Soc* **51**:279–286.

Fisher K, West M, Lomeli AM, Woodard SH, Purcell J, 2019. Are societies resilient? Challenges faced by social insects in a changing world. *Insectes Soc* **66**:5–13.

Flatt T, Tu MP, Tatar M, 2005. Hormonal pleiotropy and the juvenile hormone regulation of *Drosophila* development and life history. *Bioessays* **27**: 999–1010.

Grüter C, Czaczkes TJ, 2019. Communication in social insects and how it is shaped by individual experience. *Anim Behav* **151**:207–215.

I'Anson Price R, Grüter C, 2015. Why, when and where did honeybee dance communication evolve? *Front Ecol Evol* **3**: 125.

I'Anson Price R, Segers F, Berger A, Nascimento FS, Grüter C, 2021. An exploration of the relationship between recruitment communication and foraging in stingless bees. *Curr Zool* **67**:551–560.

Lenoir A, d'Ettorre P, Errard C, Hefetz A, 2001. Chemical ecology and social parasitism in ants. *Annu Rev Entomol* **46**:573–599.

Leonhardt SD, Menzel F, Nehring V, Schmitt T, 2016. Ecology and evolution of communication in social insects. *Cell* **164**:1277–1287.

Lockey KH, 1988. Lipids of the insect cuticle: origin, composition and function. *Comp Biochem Phsysiol B* **89**:595–645.

Nash DR, Boomsma JJ, 2008. Communication between hosts and social parasites. In: d'Ettorre P, Hughes DP, editors. *Sociobiology of Communication: An Interdisciplinary Perspective*. Oxford: Oxford University Press. 55–79.

Nehring V, Steiger S, 2018. Sociality and communicative complexity: insights from the other insect societies. *Curr Opin Insect Sci* **28**:19–25.

Nehring V, Wyatt TD, d'Ettorre P, 2013. Noise in chemical communication. In: Brumm H, editor. *Animal Communication and Noise*. New York: Springer. 373–405.

Nery D, Palottini F, Farina WM, 2021. Classical olfactory conditioning promotes long-term memory and improves odor-cued flight orientation in the South American native bumblebee *Bombus pauloensis*. *Curr Zool* **67**: 561–563.

Oi CA, van Zweden JS, Oliveira RC, Van Oystaeyen A, Nascimento FS et al., 2015. The origin and evolution of social insect queen pheromones: novel hypotheses and outstanding problems. *BioEssays* **37**:808–821.

Oi CA, Silva Rc d, Stevens I, Ferreira HM, Nascimento FS et al., 2021. Hormonal modulation of reproduction and fertility signaling in polistine wasps. *Curr Zool* **67**:519–530.

Oliveira RC, Vollet-Neto A, Oi CA, van Zweden JS, Nascimento F et al., 2017. Hormonal pleiotropy helps maintain queen signal honesty in a highly eusocial wasp. *Sci Rep* **7**:12.

Orlova M, Amsalem E, 2019. Context matters: plasticity in response to pheromones regulating reproduction and collective behavior in social Hymenoptera. *Curr Opin Insect Sci* **35**:69–76.

Richard FJ, Hunt JH, 2013. Intracolony chemical communication in social insects. *Insectes Soc* **60**:275–291.

Riddiford LM, 2012. How does juvenile hormone control insect metamorphosis and reproduction? *Gen Comp Endocrinol* **179**:477–484.

Robinson GE, 1992. Regulation of division of labor in insect societies. *Annu Rev Entomol* **37**:637–665.

Seeley TD, 1983. Division of labor between scouts and recruits in honeybee foraging. *Behav Ecol Sociobiol* **12**:253–259.

Sprenger PP, Menzel F, 2020. Cuticular hydrocarbons in ants (Hymenoptera: formicidae) and other insects: how and why they differ among individuals, colonies, and species. *Myrmecol News* **30**: 1–26.

Sprenger PP, Gerbes LJ, Sahm J, Menzel F, 2021. Cuticular hydrocarbon profiles differ between ant body parts: implications for communication and our understanding of CHC diffusion. *Curr Zool* **67**:531–540.

Tibbetts EA, Ortiz CC, Auteri GG, Simons M, Fearon ML et al., 2021. Individual recognition and individual identity signals in *Polistes fuscatus* wasps vary geographically. *Anim Behav* **176**:87–98.

von Frisch K, 1967. *The Dance Language and Orientation of Bees*. Cambridge: Harvard University Press.

Wang Q, Goodger JQ, Woodrow IE, Elgar MA, 2016. Location-specific cuticular hydrocarbon signals in a social insect. *Proc R Soc B* **283**: 20160310.

Wang Q, Goodger JQ, Woodrow IE, Chang L, Elgar MA, 2019. Task-specific recognition signals are located on the legs in a social insect. *Front Ecol and Evol* **7**: 227.