PNAS PERSPECTIVE

Diverse communication strategies in bees as a window into adaptations to an unpredictable world

Denise A. Alves[a], Ebi A. George[b], Rajbir Kaur[c], Axel Brockmann[d], Michael Hrncir[e], and Christoph Grüter[c,1]

Edited by Joan Strassmann, Washington University in St. Louis, St. Louis, MO; received January 16, 2023; accepted April 26, 2023

Communication is a fundamental feature of animal societies and helps their members to solve the challenges they encounter, from exploiting food sources to fighting enemies or finding a new home. Eusocial bees inhabit a wide range of environments and they have evolved a multitude of communication signals that help them exploit resources in their environment efficiently. We highlight recent advances in our understanding of bee communication strategies and discuss how variation in social biology, such as colony size or nesting habits, and ecological conditions are important drivers of variation in communication strategies. Anthropogenic factors, such as habitat conversion, climate change, or the use of agrochemicals, are changing the world bees inhabit, and it is becoming clear that this affects communication both directly and indirectly, for example by affecting food source availability, social interactions among nestmates, and cognitive functions. Whether and how bees adapt their foraging and communication strategies to these changes represents a new frontier in bee behavioral and conservation research.

communication | social bees | anthropogenic change

Eusocial bees, mainly the honey bees (Apini, ~11 species), bumble bees (Bombini, ~250 to 300), and stingless bees (Meliponini, ~550 to 600), have evolved diverse communication strategies that help them find and exploit resources and, in turn, shape plant communities through pollination. Bee communication impacts plant communities because communication affects which plants bees visit (1–3) and it drives bee foraging ranges (4) and promotes flower constancy, i.e., the tendency of a bee to visit flowers of the same species during a foraging trip (5), all of which impact the pollination services provided by bees. This diversity in communication and foraging strategies is linked to variation in social biology and ecology, which makes bee communication a fascinating research area to study behavioral adaptations to different lifestyles and ecological conditions. In the last decades, human activities have led to fast and pervasive environmental changes, including the loss and fragmentation of habitats, climate change, and the presence of pesticides, all of which can have a multitude of effects on bees and their central nervous system (6–9). These changes pose new challenges for bees and may require them to adjust their communication strategies through both behavioral plasticity and local adaptation. Here, we summarize how bees communicate about resources and highlight both differences in communication strategies and shared behavioral traits. We discuss the drivers of diversity in communication strategies, with a focus on social biology and ecology. Finally, we explore how rapid human-induced environmental change affects communication both directly and indirectly.

1. Diversity and Common Themes in Communication Behaviors

While eusocial bees have evolved different ways to communicate about resources, they all have the same aim, namely, to advertise the presence of profitable resources and motivate nestmates to search for these. Communication signals, therefore, usually involve an attraction component which alerts potential recruits to the presence of relevant information and a modulatory component which increases foraging motivation. In addition, some species have evolved signals that provide spatial information about food sources. This communication of spatial information can occur within or outside of the nest.

1.1. Recruitment Signals inside the Nest. A bee nest is a "noisy" environment as bees produce and encounter a multitude of acoustic, chemical, mechanical, thermal, and, in open-nesting species, visual stimuli. Thus, foragers first need to attract the attention of their nestmates (10–12). A widespread strategy to achieve this goal is to perform conspicuous, excitatory runs (also called jostling or zigzag runs) (Fig. 1). Bumble bee foragers beat their wings and release an alerting pheromone during these excitatory runs (13, 14), thereby motivating nestmates to leave the nest in search of food (13, 15).

Actual physical contact between foragers and nestmates seems to be important for forager activation in some but not in other bumble bee species (13, 14). In stingless bees, where excitatory runs are taxonomically widespread (11, 19, 21, 22) (Fig. 2), foragers bump into bystanders more frequently if they have discovered a particularly good food source (11), thereby increasing the motivation of unemployed foragers to leave

Author affiliations: [a]Department of Entomology and Acarology, Luiz de Queiroz College of Agriculture, University of São Paulo, Lausanne, 13418-900 Piracicaba, Brazil; [b]Department of Ecology and Evolution, Biophore, University of Lausanne, Bristol 1015, Switzerland; [c]School of Biological Sciences, University of Bristol BS8 1TQ, United Kingdom; [d]National Centre for Biological Sciences – Tata Institute of Fundamental Research, Bengaluru 560065, India; and [e]Department of Physiology, Bioscience Institute, University of São Paulo 05508-090 São Paulo, Brazil

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Author contributions: D.A.A., E.A.G., R.K., A.B., M.H., and C.G. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

[1] To whom correspondence may be addressed. Email: c.grueter@bristol.ac.uk.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2219031120/-/DCSupplemental.

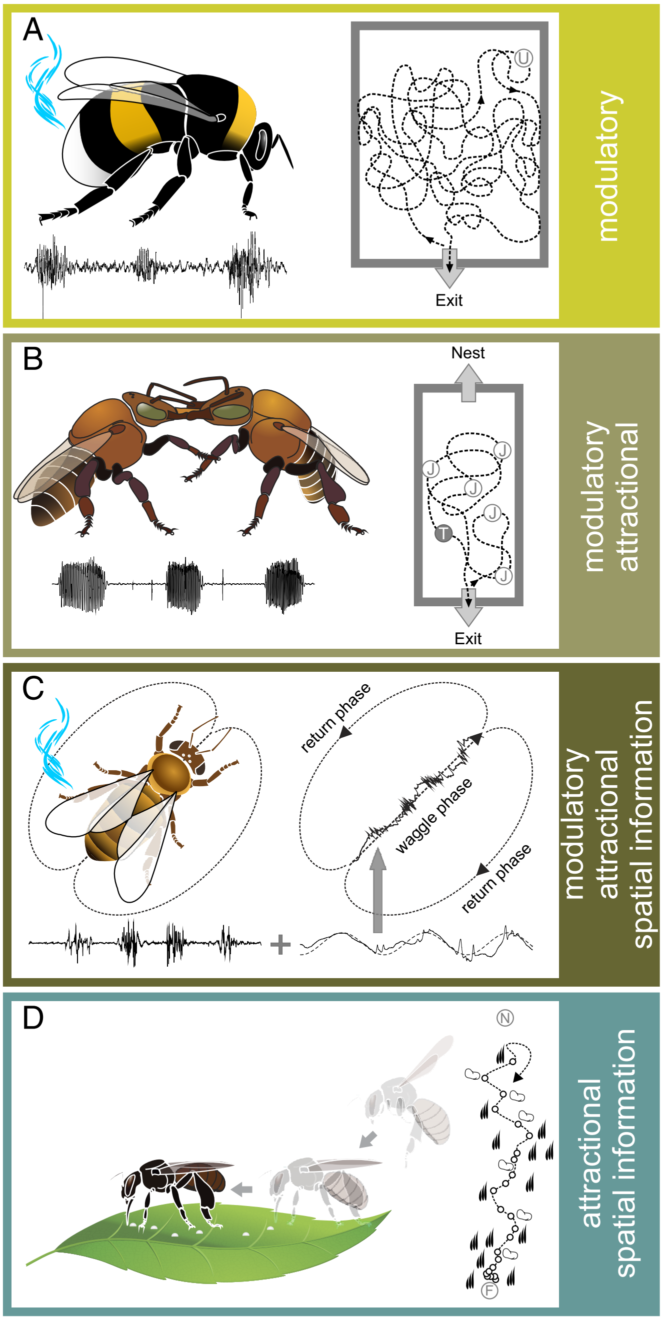

Fig. 1. Recruitment signals in social bees. Recruitment signals are produced inside (*A*–*C*) or outside of the nest (*D*). Nest-internal signals: (*A*) Bumble bees produce pulsed thoracic vibrations and emit pheromones from the tergal glands while running excitedly through the nest (Exit, position of the nest entrance/exit). Excited running often occurs after unloading food (U) into storage pots (13). (*B*) Stingless bees produce pulsed thoracic vibrations while running through the entrance structure between entrance/exit (Exit) and nest (Nest), as well as during trophallaxis (T). While running, bees bump into nestmates ("jostling", J) (11). Honey bees produce vibrations during the waggle phase of their "dance" movements, but not during the return phase. Vibrations are divided into pulsed thoracic vibrations and vibrations associated with the waggle movement. The body angle of foragers during waggling correlates with resource direction, and the duration of the waggle phase correlates with food source distance. While dancing, foragers also release cuticular hydrocarbons (16–18). Nest-external signals: some genera of stingless bees deposit pheromones from their labial glands on vegetation and stones between the food patch (F) and the nest (N) (19, 20).

the nest (23). Successful honey bee (*Apis mellifera*) foragers, similarly, enter their nest notably excited compared to their nestmates as they walk past and crawl over them (16, 24).

Another common behavior used by foragers to attract the attention of nestmates is the production of pulsed vibrations (buzzing) with their thoracic muscles (10, 17, 29, 30) (Fig. 1 and Movie S1). These buzzing sounds increase the foraging motivation of bystanders and, in doing so, the colony's foraging activity (33). The evolutionary origin of these vibration pulses may be the shivering of flight muscles for preflight warm-up (34), or pulsed buzzes that facilitate digging through the soil for nest building or emergence from subterranean nests (35). In present-day digger wasps and some solitary bees, these buzzes have additional communicatory function, informing patrolling males about the emergence of females (36) and informing females about male viability (37). In social bees, intriguingly, the temporal structure of these thoracic vibrations correlates with the profitability of food sources, thereby informing nestmates about the quality of the discovered food source (17, 33). As nestmates interact with foragers, they often learn the flower scents that cling to the body of the forager or, in the case of honey bees and stingless bees, are present in the nectar samples shared during trophallaxis (mouth-to-mouth food transfer; this behavior is absent in bumble bees) (16, 22, 38, 39). This socially facilitated learning of floral odors can have long-lasting effects on the flower choices of foragers (39–42).

In honey bees, excitatory movements have evolved into a ritualized behavioral maneuver, the famous waggle dance (16, 25, 43, 44) (Fig. 1). In the 1940s, Karl von Frisch discovered that dancing bees provide spatial information about the location of a resource encoded in the orientation of the dancer during the waggle phase of the dance (directional information) and the duration of the waggle phase (distance information) (16). Recent chemical analysis has further revealed that dancing bees also release a blend of cuticular hydrocarbons that increase forager motivation (18, 45). The waggle dance is, therefore, both a multicomponent and a multimodal signal in that it transmits information about the presence, profitability, identity, and location of a food source using different sensory modalities (12). A key feature is that the probability, duration, and intensity of dances increase with food source profitability (1, 16, 17, 46). As a result, dance followers tend to discover better food sources than bees that search for food sources through independent scouting (1). The link between dance communication and food source profitability in combination with other, less-well studied signals (such as the stop signal, the shaking signal, and the tremble dance) and individual learning capabilities enables colonies to allocate foragers dynamically in an unpredictable foraging landscape (1, 47–51).

While all honey bee species dance, there are notable differences between species in how they dance (44, 52). Dwarf honey bees (e.g., *Apis florea*), the evolutionarily most basal type of honey bee (53, 54), dance on the top of a single exposed wax comb (16, 25). The open-nesting giant honey bees (e.g., *Apis dorsata*) and the cavity-nesting honey bees (e.g., *A. mellifera*) perform dances on vertical combs (16, 25, 52). In the latter case, dancers transpose the angle between the food source and the position of the sun into an angle between their waggle phase direction and the (inverse) direction of gravity to transmit direction information. Open-nesting *A. florea* and *A. dorsata* dancers raise their abdomen while waggling (55), thereby they, literally, stick out of the crowd. This visual cue

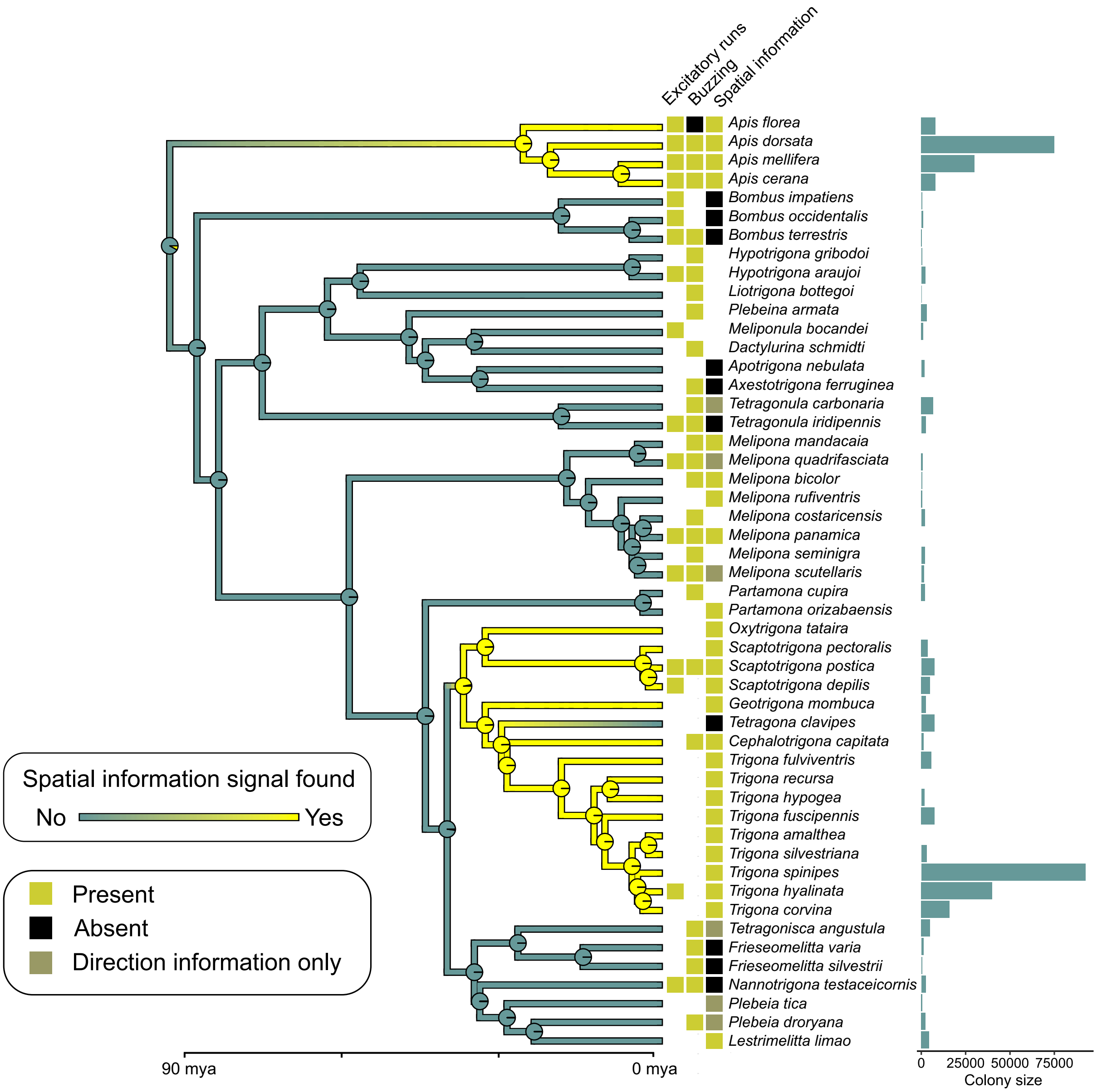

Fig. 2. Phylogenetic tree of eusocial bees (25, 26), their colony sizes (22, 27, 28), and their communication methods (11, 19, 21, 22, 29–31). Branch color indicates whether spatial information signals have been identified (either waggle dances in honey bees or pheromone trails in stingless bees) and is based on ancestral state reconstruction with an Markov chain Monte Carlo (MCMC) approach (32). Pie charts provide ancestral state estimates based on continuous-time Markov chain models (32). Boxes indicate whether evidence for the use of excitatory runs, buzzing, and spatially explicit recruitment exist. Blank space indicates an absence of evidence.

may help attract nestmates to dancers in close proximity on the crowded dance floor and dance followers may use it to detect the orientation and duration of the waggle dances.

1.2. Nest-External Communication Signals. Honey bees are not the only social bees to have evolved signals that communicate resource locations. It has long been known that some genera of stingless bees (e.g., *Cephalotrigona*, *Geotrigona*, *Oxytrigona, Scaptotrigona*, and *Trigona*) have evolved nest-external communication signals to direct recruits toward a specific food patch (19, 21, 22, 31, 56). The most striking communication system—and the only one that has been studied in detail so far—are pheromone marks and trails left on the vegetation by foragers returning to their nest from a food source (Fig. 1). The phylogenetic proximity of these genera suggests that pheromone marking evolved once in a common ancestor, ~30 to 40 Mya (22, 56) (Fig. 2).

The glandular origin of trail pheromones remained a mystery for decades, until chemical and behavioral analysis revealed that they are released from the labial glands and are transferred to the vegetation via the tongue, i.e., by licking (Fig. 1) (20, 56, 57). The chemical composition of these pheromones is species-, population-, and even colony-specific, but usually comprises highly volatile substances (56, 58), which allows the chemicals to be perceived over long distances. Pheromone deposition is most frequent at and near the food source and decreases with increasing distance from the resource, which provides further directional information (polarity) (31, 59). Some species (e.g., *Trigona spinipes*) lay relatively short scent trails of up to 30 m (59), while others (e.g., *Trigona amalthea*) can lay chemical trails of several hundred meters length (60).

Pheromone trails as a spatially explicit communication signal have both advantages and disadvantages compared to the honey bee waggle dance. Pheromone marks lead to a rapid and efficient buildup of foragers at a food source (19), and a chemical trail might be especially useful in a stratified environment, such as a tropical rainforest. On the contrary, chemical trails are also more "public" and, therefore, prone to eavesdropping and exploitation by competitors (61, 62). This could represent a major cost for ecologically subordinate species. The waggle dance, on the contrary, is more concealed from the outside world, especially in cavity-nesting honey bees and, unlike pheromone trails, is protected from environmental factors (e.g., wind and heat) (Section 3). The geographic and ecological context in which the waggle dance evolved—tropical forest in Asia (63) versus open, patchy habitats in Europe (64)—remains a matter of debate (25).

Despite recent progress, stingless bee communication remains full of puzzles. Artificial feeder array studies show that foragers of several species that do not use pheromone marks and trails are able to steer recruits in the direction of a food source. Yet, how they do so remains unknown. In some cases, recruits do not appear to obtain any distance information (65–67) (Fig. 2). Local enhancement (i.e., the use of olfactory or visual cues provided by bees at the feeding site) may, in part, be responsible for this biased recruitment (68). Another mysterious case is *Partamona*, a Neotropical genus with the ability to mass-recruit to specific locations without any obvious signs of nest-external communication (69). In these cases, aerial odor trails created by flying foragers or visual piloting by foragers have been proposed as signaling strategies (19, 60), but these putative mechanisms require confirmation.

Honey bees are known to use a volatile and attractive pheromone released from their Nasonov gland (16), primarily during the swarming process (70). Nasonov signaling has also been observed during foraging, particularly at water and artificial nectar sources (16, 71), but it attracts recruits mainly to water and scentless food sources. Since it is not usually observed when bees forage at natural food sources (72), its importance for foraging at natural food sources remains unclear (73).

2. New Insights into the Drivers of Diversity in Communication Behavior

What explains this diversity in bee communication strategies and why do many species exploit resources without communicating their location? Tropical habitats, in particular, are home to a diverse eusocial bee fauna and tropical environments represent potential hotspots to study and better understand the evolution of diverse communication behaviors. Empirical and theoretical researches in the last two decades have highlighted the importance of two drivers of diversity in communication strategies, variation in social biology and ecology.

2.1. Social Biology as Drivers of Communication Diversity. Colony size varies by several orders of magnitude in social insects and largely determines the size of the forager pool (74). This, in turn, shapes the types of communication signals used during recruitment. In ants, species with small colonies often rely on solitary foraging, species with medium-sized colonies preferentially use mechanical recruitment processes like tandem running, and species with large colonies employ pheromone trails (75, 76). Small colonies lack the numbers to maintain effective pheromone trails (77) and foragers of small colonies using tactile signals experience greater time delays (i.e., opportunity costs) (78). Similar colony size–related patterns are found in eusocial bees. Bumble bees usually establish small annual colonies and, while foragers perform excitatory runs and thoracic vibrations inside their nest, they do not share food by mouth-to-mouth feeding and workers largely forage solitarily (27, 79) (Fig. 1). Communication signals that provide spatial information have evolved in parallel in stingless bees and honey bee species (16, 22, 27), which typically have larger colony sizes than those of bumble bees (Fig. 2). Furthermore, a recent comparative analysis showed that, among stingless bees, pheromone laying is found in species with larger colony sizes, while species with smaller colony sizes often forage solitarily (22).

Nesting biology is another potential driver of variation in communication strategies, and we propose that it explains why the waggle dance evolved in honey bees, but did not evolve in stingless bees or bumble bees. Social bees use sky compass and visual odometer information to track their position relative to their nest (so-called path integration), which they combine with view-based learning to navigate and travel between nest and food sources (16, 80). Open nesting, the ancestral nesting habit in honey bees (53, 54), may have been the necessary condition for the evolution of the waggle dance as it allowed a forager dancing on a horizontal surface (as done by the evolutionarily basal dwarf honey bees) to orientate the waggle movement toward the direction of the food source using the flight directional information (81). Waggle dancers on horizontal surfaces require sky view to perform oriented dances (16). Without celestial cues, dances become disoriented and, therefore, no longer provide useful spatial information (16). From these dances in open-nesting honey bees, waggle dances that transpose path integration information into an angle on vertical surfaces and in cavities could evolve (16, 25, 52, 54). Since only honey bees build open nests and with a view of the sky compass (22, 27), they were the only social bees with an opportunity to evolve this particular form of communication. Bumble bees can perform vector navigation and orient to visual cues while walking in small experimental arenas using artificial light sources (82), and it would be fascinating to explore whether bumble bees orient their runs inside their nest toward a food source using the sky compass if tested in an open nesting condition. Such an ability to spontaneously orient their locomotor patterns using the sky compass could be viewed as a preadaptation that made the evolution of waggle dances on a horizontal surface possible.

We have mainly focused on communication about food sources, but social bees also communicate about water sources (for cooling), nest-building material, and nesting sites (16, 22, 27, 83). Tropical honey bees, in particular, regularly relocate their nests, often in synchrony with flowering periods and rainy seasons (54, 84, 85). The benefits of these colony migrations in tropical honey bees could have been an additional factor selecting for the evolution of spatially explicit communication that allowed colonies to migrate efficiently toward a new nesting site (16, 19, 25).

2.2. Ecology as Drivers of Communication Diversity. Eusocial bees inhabit environments ranging from the arctic tundra to tropical rainforests and this affects how resources are distributed in space and time. Empirical and, more recently, theoretical studies suggest that the value of communication about food resource locations depends on the spatiotemporal availability of food sources (86–91), but see ref. (92). These studies highlight that communication about food source locations is not beneficial per se and explains why some species communicate about resources, while many others engage in solitary foraging. Theoretical studies predict that spatial information is beneficial when food sources vary in quality, and when high-quality resources are difficult to find by independent search, e.g., because they are clustered or far away (78, 86, 88, 89). When food sources vary little and are easy to find, foragers should search independently and avoid the opportunity costs that result from waiting for social information (93). While these predictions await further experimental examination under field conditions, there is preliminary empirical support for a clustering effect in *A. mellifera*: Experimentally disrupting dance communication in two *A. mellifera* colonies had no negative effect on foraging success in a temperate habitat but reduced foraging success in two colonies in a tropical dry forest in India (87). Clustering and food source variability are likely to be higher in the tropics where mass-flowering trees are an important resource for social bees and where a more diverse flora means that bees have access to a highly diverse foraging landscape (22, 94, 95). A more recent study found no effect of environmental heterogeneity on colony foraging success in Central European agricultural landscapes due to disruption of the dance communication (92). Even without spatial communication, colonies in the tropics are likely to benefit from communication signals that lead to a rapid increase in their general foraging activity when foraging conditions become favorable, such as after heavy showers during the rainy season.

An intimate link between the communication strategy of a species and foraging ecology has recently also been revealed in the "dance dialects" of honey bees, i.e., the way different species encode distance information in their dances (96, 97). *Apis* species and populations that forage at shorter distances, due to a high food availability, show a larger change in the waggle phase duration with increasing food source distance compared to honey bees that forage at greater distances. This allows foragers to communicate food source locations with greater spatial resolution, thereby helping recruits discover the correct patch in the dense and variable foraging environments of tropical Asia.

Another important ecological factor with implications for communication strategies is food source competition (2, 3, 22, 98). Most eusocial bees are generalist foragers, i.e., they visit a wide range of flower species, which results in the overlap of dietary niches of colonies and, therefore, competition (2, 22, 98, 99). In highly competitive environments, spatially explicit communication allows colonies to rapidly increase the number of foragers at a food patch and, thereby, exclude competitors (2, 3, 22). Species without spatial communication may be forced to switch to alternative resources, often more dispersed plants with fewer flowers (2, 3, 22, 100). The ability to recruit and monopolize food patches also depends on colony size (2, 101), highlighting that ecological factors often interact with biological traits to shape communication strategies.

3. Anthropogenic Change and Communication

Human activities have dramatically changed the habitats bees inhabit, and behavioral strategies that have helped eusocial bees to be successful might no longer be equally beneficial or even have net costs in highly modified environments, adding to the unprecedented challenges that bees face (6–8). While anthropogenic effects on communication behaviors may not have a significant impact on colony fitness of social bees per se, they have the potential to put further pressure on colonies facing a cocktail of stressors. Understanding if and how behavioral strategies are affected by anthropogenic change is a rapidly growing research area (102–104) and recent research on social bees has started to reveal how bees respond to these challenges.

3.1. Habitat Fragmentation and Land Use Change. Habitat fragmentation and urbanization changes the distribution, diversity, quality, and temporal availability of resources. As discussed above, this will affect the value of communication about resources. In temperate regions, urban areas often provide diverse and continuous food resources for bees, mainly in dispersed residential gardens (105, 106), which in turn is beneficial for many wild bees (107). There is evidence that spatial communication might lose value and could even be maladaptive in such urban environments. In a highly modified urban European environment, honey bee (*A. mellifera*) colonies with experimentally disrupted dances were more successful than colonies with normal waggle dances (108). Furthermore, colonies in urban areas found food sources closer to their nest compared to colonies in less urban environments (109), which is likely to lower the value of spatial information encoded in the waggle dance (86). A continuous availability of a diverse mix of native and exotic flowers in urban gardens (106) is also likely to reduce the benefits of other communication behaviors that modulate colony-foraging activity.

The fragmentation of natural habitat could have the opposite effect if it creates isolated patches of high-quality food sources. Spatial communication helps colonies to exploit isolated patches more efficiently (110). In agricultural settings, on the contrary, food source diversity is often lower (105) and highly rewarding food sources are available only during certain times of the year (111), which likely lower the value of spatial communication. It is important to note that while communication of spatial information might be costly in one environment and beneficial in another, colonies might collect overall more food in the first environment if it offers a continuous supply of food source in proximity to the nest. This, in turn, would lead to relaxed selection on communication precision. In turn, highly fragmented environments might lower colony success if food source abundance is no longer sufficient even if the food source distribution makes communication beneficial.

3.2. Climate Change. Climate change can affect bee communication either directly, by impacting communication signals, or indirectly, by changing the quality and availability of resources, which in turn affects the efficiency of foraging and recruitment strategies (6, 112).

While the impact of climate warming on recruitment signals in bees has not yet been directly investigated, such effects are plausible based on what is known about bee physiology and communication signal properties. In *A. mellifera*, the "excitement" of foragers is tightly linked to their body temperature (113). Since bees are not perfectly endothermic, their body temperature increases with ambient temperature (114, 115), and an elevated body temperature of returning foragers (116, 117) may be translated into more intense recruitment behavior, while the warmer nectar could lead to more efficient learning of food odors (118). Extreme heat events could also have delayed, negative effects on recruitment given that elevated temperatures during brood development result in reduced sensitivity to sucrose rewards later in life (119), which is likely to dampen the motivation of bees to forage and communicate (1, 16, 120). These temperature effects are especially relevant for tropical stingless bees and honey bees, which tend to have a reduced ability to control brood area temperature compared to temperate honey bees (22, 121). Temperature effects on reward perception, body temperature, and their interaction with body size (see also ref. 2) deserve further investigation to better predict the direct impact of climate warming on bee foraging behavior.

Atmospheric changes may also affect pheromone communication in different ways. First, reported levels of increases in oxidative greenhouse gases, like ozone, have been shown to alter the chemical structure of pheromones through oxidation, thereby interfering with communication (122–124). Second, increasing ambient temperatures have been shown to significantly increase pheromone decay and, therefore, pheromone following by recruits in ants (125). Differential evaporation rates for different compounds of the scent bouquet may further alter the chemical profile of the pheromones (126). These findings suggest that pheromone communication based on long-range chemical signaling is likely to be negatively impacted by climate change, but research is needed to test the susceptibility of stingless bee pheromones to increase in temperature, greenhouse gases, and other air pollutants.

Global warming can also affect communication strategies indirectly. Changes in ambient temperature affect the window of availability of critical resources, both during the day and over the year; the longevity of flowers; the abundance of simultaneously blooming individuals; as well as the production of floral rewards such as nectar and pollen (127, 128). These temperature-driven changes, however, vary greatly between plant species and, thus, the effect of climate warming on the availability of floral rewards cannot be generalized. If floral resources decrease in abundance and longevity, strategies that provide spatial information and allow for rapid changes in colony-foraging activity should be more beneficial than those that do not. After discovering a food source, colonies can direct their foraging force toward a specific patch, minimizing time and energy costs associated with random search.

3.3. Pesticides. Social bees gather large amounts of floral and nesting resources to maintain their society and, as a result, they are exposed to pesticides commonly used in both agricultural and urban landscapes (8, 129, 130). In the last years, a number of studies have found evidence that pesticides and their metabolic by-products have varied negative effects on physiological, behavioral, and cognitive traits of bees (8, 9, 130), many of which are important for communication. Effects with potential consequences for communication include the impairment of key cognitive functions, such as learning (9) and navigation (131); changes in sensory perception, such as reward perception (132, 133); and the performance of communication itself (133, 134). Furthermore, pesticides can affect social interactions, including antennation (135), exchange of food (135, 136), and locomotion (137).

Disruptions of cognitive processes and/or motor functions due to pesticide exposure can negatively affect communication in different ways. After ingesting sublethal doses of the neonicotinoid imidacloprid, honey bee foragers reduced their dance communication (133) and their dance became less accurate (138), which will reduce a colony's ability to exploit high-quality food sources. In the stingless bee *Melipona quadrifasciata*, ingestion of commonly used pesticides by adult workers reduced trophallaxis and antennation (135), which are important in their communication process (Fig. 1 and Movie S1). Worryingly, pesticides are commonly found in nest food stores (9), thereby prolonging their impact.

Pesticide exposure can also induce subtle changes in cuticular hydrocarbon profiles, which in turn affect social interactions. A fungus-based biopesticide was found to affect social recognition of nestmates in both honey bees (139) and a stingless bee (140). While honey bee foragers received less aggression by unrelated guards, *Tetragonisca angustula* stingless bee foragers were increasingly aggressed by their own guards after exposure to the biopesticide. Both studies highlight the potential of pesticides to disrupt and change social interaction networks that are critical for colony functioning.

The work discussed in this perspective highlights that the study of communication in eusocial bees provides fascinating insights into the behavioral adaptations of eusocial bees to the environments they inhabit while also offering many avenues for future research into how bee colonies communicate. Communication behaviors help colonies exploit resources in an unpredictable world, and more research is needed to understand how anthropogenic change affects communication. Social bees show an impressive ability to adjust their behavior to novel situations, but it remains to be seen whether this plasticity is adaptive or comes at an evolutionary cost.

Data, Materials, and Software Availability. Previously published data used for this work can be found in refs. (22) (Table 1.3), (27) (Table 6.1) and (28).

ACKNOWLEDGMENTS. We thank two anonymous reviewers for comments that helped improve this article. D.A.A. was funded by a grant of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grant: 164743/2020-0). E.A.G. acknowledges funding from the European Research Council (Advanced Grant resiliANT awarded to Laurent Keller) and the University of Lausanne. A.B. was supported by institutional funds from the National Centre for Biological Sciences (NCBS) of the Tata Institute of Fundamental Research (No. 12P4167) and the Department of Atomic Energy, Government of India (No. 12-R&D-TFR-5.04-0800 and 12-R&D-TFR-5.04-0900). M.H. was funded by a CNPq grant (311590/2019-5). R.K. was funded by the Biotechnology and Biological Sciences Research Council (grant: BB/W001977/1).

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