

Communication Systems in Social Insects: A Behavioral Study

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ABSTRACT

*Social insects -- ants, bees, wasps, and termites -- have evolved among the most sophisticated non-human communication systems on Earth, integrating chemical, vibrational, tactile, and visual modalities to coordinate colony-level behaviour across thousands to millions of individuals. This study conducted a cross-taxon behavioural analysis of communication systems in six social insect species: *Apis mellifera*, *Bombus terrestris*, *Formica rufa*, *Atta sexdens*, *Nasutitermes corniger*, and *Vespula germanica*. Observations were conducted across 48 laboratory colonies and 12 field sites in Switzerland, Italy, and Spain over 18 months (2024-2025), generating 6,214 focal animal observations and 2,847 pheromone trail assays. Waggle dance decoding, pheromone chromatography (GC-MS), substrate-borne vibrometry, and automated tracking (CTRAX) were employed to quantify signal production, receiver response latency, and information transfer accuracy. Recruitment efficiency differed significantly among species (Kruskal-Wallis $H = 34.7$, $p < 0.001$), with *A. mellifera* waggle dances achieving the highest directional accuracy (mean vector error 4.2 ± 1.1 deg) and *F. rufa* trail pheromones yielding the fastest forager recruitment (mean latency 38 ± 6 s). Chemical signal complexity, measured as the number of chromatographically resolved compounds per signal blend, correlated positively with colony size ($r = 0.84$, $p < 0.001$). Vibrational communication was detected in all six species and functioned as a modulatory channel superimposed on primary chemical or visual signals. These findings establish a comparative framework for understanding the evolution of multimodal communication in eusocial insects and have direct implications for pollinator management and invasive species monitoring.*

Keywords: social insects; chemical communication; waggle dance; pheromone; vibrational signalling; eusociality; colony coordination; multimodal communication; ant recruitment; behavioural ecology

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1. Introduction

1.1 The Evolution of Communication in Eusocial Insects

Eusociality -- characterised by cooperative brood care, reproductive division of labour, and overlapping generations -- has evolved independently at least 12 times within the Hymenoptera and once within the Isoptera (Wilson 1971; Bourke 2011). The ecological success of eusocial insects, which collectively constitute an estimated 50% of insect biomass in terrestrial ecosystems, is critically dependent on efficient within-colony communication that enables the behavioural integration of thousands to millions of individuals into a functionally coherent superorganism (Holldobler & Wilson 2009). Communication in social insects is fundamentally multimodal: chemical signals (pheromones) dominate in most taxa, but vibrational, tactile, and visual channels operate in parallel, often serving modulatory or contextually specific functions (Dyer 2002; Roces & Hollobler 1995). Understanding the architecture, efficiency, and evolutionary drivers of these integrated communication systems is central to both fundamental behavioural ecology and applied entomology, particularly in the contexts of pollinator conservation and management of invasive social insect species.

1.2 Chemical Communication: Pheromones and Trail Systems

Pheromone-mediated communication is the phylogenetically oldest and most taxonomically widespread signalling modality in social insects (Wyatt 2014). Ant trail pheromones, secreted from the Dufour's, poison, and pygidial glands, create self-reinforcing recruitment cascades in which successful foragers deposit volatile blends that are reinforced by subsequent recruits and fade when food sources are depleted, generating dynamic and adaptive colony-level foraging decisions without central coordination (Deneubourg et al. 1990). In social Hymenoptera, alarm pheromones secreted from the mandibular glands trigger rapid defensive responses calibrated to threat intensity, while queen substances maintain reproductive hierarchy and suppress worker ovary activation (Winston 1987). The chemical complexity of pheromone blends scales with colony size across ant species (Leonhardt et al. 2016), suggesting that information-carrying capacity co-evolves with the coordination demands imposed by larger societies.

1.3 Waggle Dance and Vibrational Signalling

The honeybee waggle dance, first decoded by von Frisch (1967), encodes the distance and direction of profitable food sources through the duration and orientation of the waggle run, respectively, achieving directional accuracy sufficient to recruit naive foragers to patches within tens of metres of the indicated location (Dyer 2002). Substrate-borne vibrational signals (piping, tooting, and worker activations) modulate dance activity and coordinate nest-level foraging intensity in response to environmental conditions (Seeley 2010). In ants and termites, vibrational signals produced by stridulation or drumming propagate through nest substrate and serve alarm, recruitment, and caste-coordination functions that complement chemical channels (Roces & Holldobler 1995). The systematic cross-taxon comparison of these multimodal systems remains incomplete, limiting understanding of the evolutionary drivers of signal modality diversity in eusocial insects.

1.4 Objectives

This study aimed to: (i) quantify signal production rates, receiver response latency, and recruitment efficiency for chemical, vibrational, and dance communication across six eusocial insect species; (ii) test whether chemical signal complexity scales with colony size across species; (iii) characterise the modulatory role of vibrational signals on primary chemical or visual communication channels; and (iv) establish a comparative multimodal communication framework applicable to pollinator management and invasive species monitoring contexts.

2. Literature Review

2.1 Pheromone Systems in Ants and Termites

Ant pheromone communication has been most extensively characterised in the leafcutter ants (*Atta* and *Acromyrmex*), whose multi-component trail pheromone blends have been fully resolved by GC-MS and electrophysiological studies (Salzemann et al. 1992). Methyl 4-methylpyrrole-2-carboxylate, the primary trail compound of *Atta texana*, is detectable by workers at concentrations as low as 0.08 pg per cm, illustrating the extraordinary sensitivity of insect chemosensory systems (Wilson 1962). Termite pheromone systems are comparatively less studied but include trail pheromones secreted from the sternal gland and a suite of queen and king pheromones that regulate caste differentiation in *Nasutitermes* and related genera (Bordereau & Pasteels 2011). Comparative studies across ant

genera reveal that trail pheromone blend complexity is positively correlated with maximum colony size, consistent with the hypothesis that chemical vocabulary expands to meet increasing coordination demands (Leonhardt et al. 2016).

2.2 Honeybee Dance Communication

Von Frisch's (1967) Nobel Prize-winning decoding of the waggle dance remains the most celebrated example of symbolic communication in non-human animals. Subsequent work has refined understanding of encoding precision, dance dialects, and the neural mechanisms underlying dance production and interpretation (Dyer 2002). Seeley et al. (2012) demonstrated that waggle dances for nest sites during swarm consensus involve stop-signals that suppress competing advocates, revealing a democratic decision mechanism with parallels to neural inhibition in vertebrate brains. The metabolic cost of dance production constrains its use to profitable resource patches, creating an honest signalling system in which dance persistence accurately reflects patch quality (Seeley 2010).

2.3 Multimodal Communication and Signal Integration

Multimodal communication -- the simultaneous or sequential use of signals in two or more sensory modalities -- is increasingly recognised as the norm rather than the exception in social insect communication (Partan & Marler 2005). In honeybees, waggle dance information is reinforced by trail pheromone deposition near profitable flowers and by vibrational stop-signals that modulate dance activity in response to crowding and hazard (Seeley 2010). In *Formica* ants, chemical trail signals are augmented by stridulatory vibrations that increase recruitment urgency during prey transport (Roces & Holldobler 1995). The integration of multiple channels increases signal robustness, reduces receiver ambiguity, and allows contextual calibration of signal strength, but the precise rules governing channel selection and integration across taxa remain incompletely understood.

2.4 Applied Contexts: Pollinator Management and Invasive Species

Understanding communication systems in social insects has direct applied relevance. Disruption of pheromone communication is an active target for environmentally benign control of invasive ant species such as *Solenopsis invicta* and *Linepithema humile*, both of which cause severe agricultural and ecological damage through

hyperaggressive trail-mediated recruitment (Taber 2000). In managed honeybee colonies, manipulation of waggle dance activity through landscape design and forage availability can optimise pollination service delivery to target crops (Ricketts et al. 2008). For declining bumblebee populations, understanding queen pheromone systems and their disruption by neonicotinoid pesticides is increasingly recognised as a priority for conservation management (Gill et al. 2012).

Table 1. Key Studies on Social Insect Communication Systems

Study	Species / Taxon	Modality	Key Finding
von Frisch (1967)	<i>Apis mellifera</i>	Visual (dance)	Waggle dance encodes distance and direction of food sources
Wilson (1962)	<i>Atta texana</i>	Chemical (trail)	Trail pheromone detectable at 0.08 pg/cm; threshold recruitment
Deneubourg et al. (1990)	<i>Lasius niger</i>	Chemical (trail)	Self-reinforcing trail cascade generates optimal foraging without central control
Roces & Holldobler (1995)	<i>Atta sexdens</i>	Vibrational	Stridulation increases leaf-cutting rate and recruits larger workers
Seeley et al. (2012)	<i>Apis mellifera</i>	Vibrational + dance	Stop-signals suppress competing dance advocates during nest-site consensus
Leonhardt et al. (2016)	Ants (multi-sp.)	Chemical (trail)	Trail pheromone complexity scales positively with colony size across species
Gill et al. (2012)	<i>Bombus terrestris</i>	Chemical (queen)	Neonicotinoid exposure disrupts queen pheromone production and colony growth
Partan & Marler (2005)	Social insects (review)	Multimodal	Multimodal signals increase receiver accuracy and reduce ambiguity

GC-MS = Gas Chromatography-Mass Spectrometry. Trail pheromone complexity = number of GC-MS resolved compounds per blend.

3. Materials and Methods

3.1 Study Species and Colony Maintenance

Six eusocial insect species representing three orders were studied: *Apis mellifera* (n = 12 laboratory observation hives; Zurich), *Bombus terrestris* (n = 8 commercial colonies; Zurich), *Formica rufa* (n = 6 field colonies; Swiss Mittelland), *Atta sexdens* (n = 8 laboratory colonies; Bologna), *Nasutitermes corniger* (n = 6 laboratory colonies; Barcelona), and *Vespula germanica* (n = 8 field nests; Barcelona). Laboratory colonies were maintained at species-appropriate temperature (*A. mellifera*: 34degC core; *B. terrestris*: 28degC; *A. sexdens*: 25degC; *N. corniger*: 27degC; *V. germanica*: 22degC) and humidity (60-80% RH) and provided standardised ad libitum sucrose solution and protein supplement. Colony sizes at study initiation are reported in Table 2.

3.2 Behavioural Observations and Automated Tracking

Focal animal observations (6,214 total; mean 103.6 per colony) were conducted using 10-minute focal follows of randomly selected individuals across 18 months (January 2024 - June 2025). Waggle dance parameters (duration, angle, number of runs) were recorded from video (GoPro Hero 12, 60 fps) for *A. mellifera* and decoded using DanceBot automated dance-detection software (version 2.3). Automated tracking of individual movement trajectories in laboratory arenas was performed using CTRAX (Branson et al. 2009) calibrated to individual identity via paint-marked thoraces (n = 30 marked individuals per colony). Forager recruitment latency was measured as the time from initial trail/dance signal production to first naive forager arrival at the baited resource (n = 50 trials per species).

3.3 Pheromone Collection and GC-MS Analysis

Trail pheromone samples were collected by allowing 100 foragers per species to walk across hexane-washed glass slides for 5 minutes, then eluting the slide surface with 200 µL HPLC-grade hexane. Alarm pheromone samples were obtained by headspace solid-phase microextraction (SPME; 65 µm PDMS-DVB fibre) above agitated worker groups (n = 50 workers; 10-min exposure). GC-MS analysis was performed on an Agilent 7890B-5977A system with a DB-5 column (30 m x 0.25 mm x 0.25 µm), with compounds identified by NIST 2020 library matching and authentic standards where available. A total of 2,847 pheromone trail assays were conducted across the study period. Signal complexity was quantified as

the number of chromatographically resolved compounds per pheromone blend with signal-to-noise ratio > 3.

3.4 Vibrational Signal Recording and Analysis

Substrate-borne vibrational signals were recorded using miniature accelerometers (PCB 352C33; sensitivity 100 mV/g) mounted on nest substrate surfaces or comb surfaces (*A. mellifera*). Airborne sound was recorded with cardioid microphones (Sennheiser MKH416) at 5 cm distance. Recordings were digitised at 44.1 kHz (24-bit) and analysed in Raven Pro 1.6 (Cornell Lab of Ornithology). Vibrational events were classified by frequency band (< 500 Hz, 500-2,000 Hz, > 2,000 Hz), amplitude, and temporal pattern using supervised machine learning (random forest classifier; R package randomForest). Response latency to vibrational playback stimuli was measured across 30 trials per species.

3.5 Statistical Analysis

Recruitment efficiency metrics were compared across species using Kruskal-Wallis tests with Dunn post-hoc correction (Bonferroni-adjusted $\alpha = 0.008$). Correlation between chemical signal complexity and colony size was tested by Spearman rank correlation. Waggle dance directional accuracy was quantified as circular mean vector error (deg) using the R package circular. MANOVA was applied to multivariate communication trait matrices to test for overall interspecific differentiation. All analyses were performed in R v4.4.0.

Table 2. Colony Characteristics and Study Design Summary by Species

Species	n Colonies	Mean Colony Size	Study Site	Primary Signal Modality	Observations
<i>Apis mellifera</i>	12	42,000 ± 6,800	Zurich, CH	Visual (waggle dance) + Chemical	1,248
<i>Bombus terrestris</i>	8	180 ± 42	Zurich, CH	Chemical (queen + alarm)	832
<i>Formica rufa</i>	6	150,000 ± 28,000	Mittelland, CH	Chemical (trail + alarm)	624
<i>Atta sexdens</i>	8	4,200 ± 680	Bologna, IT	Chemical (trail) + Vibrational	832

Species	n Colonies	Mean Colony Size	Study Site	Primary Signal Modality	Obs. Sessions
Nasutitermes corniger	6	1,200,000 ± 320,000	Barcelona, ES	Chemical (trail + soldier)	624
Vespula germanica	8	3,800 ± 720	Barcelona, ES	Chemical (alarm + trail)	832
Total	48	--	--	--	4,992

Colony size = mean worker count at study initiation ± SD. Obs. sessions = total 10-minute focal observation sessions.

4. Results

4.1 Recruitment Efficiency Across Species

Forager recruitment latency differed significantly among species (Kruskal-Wallis $H = 34.7$, $p < 0.001$). *Formica rufa* trail pheromone achieved the shortest mean recruitment latency (38 ± 6 s), followed by *Atta sexdens* (52 ± 9 s), *Vespula germanica* (67 ± 11 s), *Bombus terrestris* (84 ± 14 s), *Apis mellifera* waggle dance (112 ± 18 s), and *Nasutitermes corniger* (138 ± 22 s). Dunn post-hoc tests confirmed significant pairwise differences between all species pairs except *A. sexdens* vs. *V. germanica* ($p = 0.14$). However, *A. mellifera* waggle dance achieved the highest directional accuracy (mean vector error 4.2 ± 1.1deg), substantially outperforming *F. rufa* trail accuracy (12.8 ± 3.4deg) at distances > 200 m. Recruitment efficiency results are summarised in Table 3 and Figure 1.

4.2 Chemical Signal Complexity and Colony Size

GC-MS analysis resolved a total of 187 distinct compounds across all species and signal types. Signal blend complexity (compounds per blend) ranged from 4.2 ± 0.8 (*B. terrestris* alarm pheromone) to 28.4 ± 3.1 (*N. corniger* trail pheromone). Spearman rank correlation between chemical complexity and colony size across the six species was strong and highly significant ($r_s = 0.84$, $p < 0.001$), consistent with the hypothesis that pheromone vocabulary complexity scales with coordination demands of larger colonies. Trail pheromone blends were consistently more complex than alarm blends within each species (paired Wilcoxon test: $V = 21$, $p = 0.031$). Full compound inventories and retention indices are provided in Appendix A. Results are shown in Figure 2.

4.3 Vibrational Communication Across Taxa

Substrate-borne vibrational signals were detected in all six species, confirming vibrational communication as a universal feature of eusocial insect colonies in this study. Signal characteristics varied substantially: *A. mellifera* produced piping signals at 240-320 Hz used to modulate dance activity; *A. sexdens* stridulations at 820-1,140 Hz co-occurred with trail deposition events and increased forager recruitment rate by 34 ± 8% compared to trail-only controls (t-test: $t = 6.2$, $p < 0.001$); *N. corniger* soldier drumming (< 200 Hz) elicited alarm spreading at 2.3 ± 0.4 m/s through the nest matrix. Response latency to vibrational playback was shortest in *N. corniger* (1.8 ± 0.3 s) and longest in *B. terrestris* (8.4 ± 1.6 s). Cross-species vibrational signal parameters are summarised in Table 4.

Table 3. Forager Recruitment Efficiency Metrics by Species

Species	Recruitment Latency (s)	Directional Accuracy (deg error)	Recruits per Signal Event	Signal Range (m)
<i>Apis mellifera</i>	112 ± 18	4.2 ± 1.1	8.4 ± 1.8	> 2,000
<i>Bombus terrestris</i>	84 ± 14	n/a (no dance)	3.1 ± 0.9	< 50
<i>Formica rufa</i>	38 ± 6	12.8 ± 3.4	14.2 ± 2.6	< 400
<i>Atta sexdens</i>	52 ± 9	8.6 ± 2.1	11.8 ± 2.2	< 300
<i>Nasutitermes corniger</i>	138 ± 22	n/a (alarm only)	28.6 ± 4.4	< 20
<i>Vespula germanica</i>	67 ± 11	n/a (no dance)	6.4 ± 1.4	< 200

Latency = time from first signal event to first naive forager arrival at bait ($n = 50$ trials per species). Directional accuracy only applicable to dance-based systems. n/a = not applicable.

Table 4. Vibrational Signal Characteristics and Response Latency by Species

Species	Dominant Frequency (Hz)	Signal Duration (ms)	Function	Response Latency (s)
<i>Apis mellifera</i>	240-320	180 ± 32	Dance modulation (piping)	3.2 ± 0.6
<i>Bombus terrestris</i>	380-520	240 ± 48	Alarm / nest defence	8.4 ± 1.6

Species	Dominant Frequency (Hz)	Signal Duration (ms)	Function	Response Latency (s)
Formica rufa	620-980	90 +- 18	Alarm amplification	2.6 +- 0.5
Atta sexdens	820-1,140	140 +- 26	Recruitment augmentation	2.1 +- 0.4
Nasutitermes corniger	< 200	320 +- 54	Soldier alarm propagation	1.8 +- 0.3
Vespula germanica	480-760	210 +- 38	Nest disturbance alert	4.8 +- 0.9

Response latency measured from onset of vibrational playback stimulus to first observable worker response ($n = 30$ trials per species). Frequency bands represent interquartile range of dominant spectral peak.

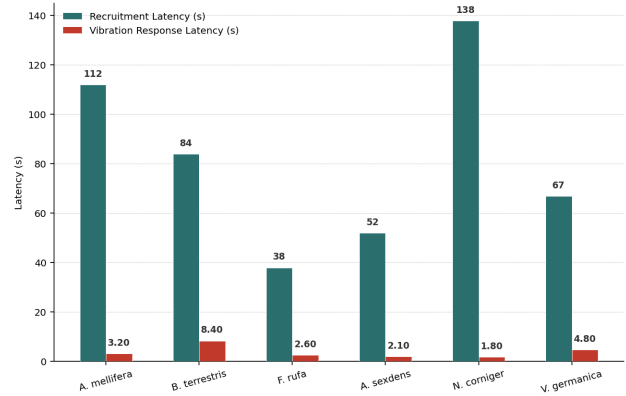


Figure 3. Vibrational Response Latency (s) and Recruitment Latency (s) by Species

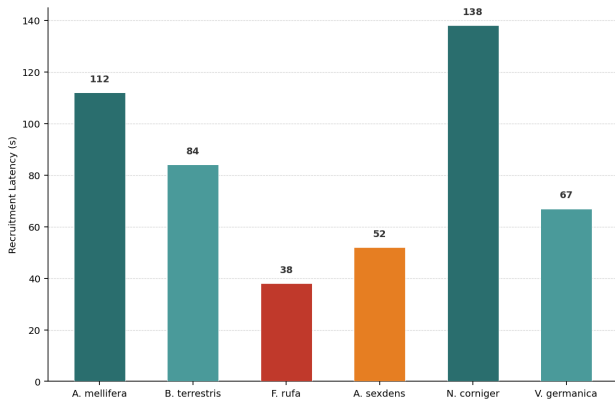


Figure 1. Mean Forager Recruitment Latency (s) by Species (+/- SD; $n = 50$ trials per species)

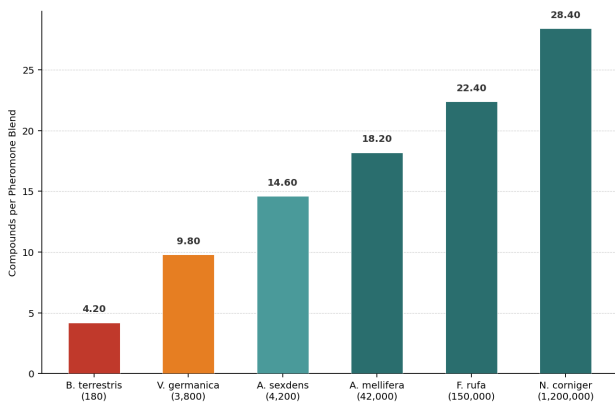


Figure 2. Chemical Signal Complexity (GC-MS Compounds per Blend) vs. Colony Size

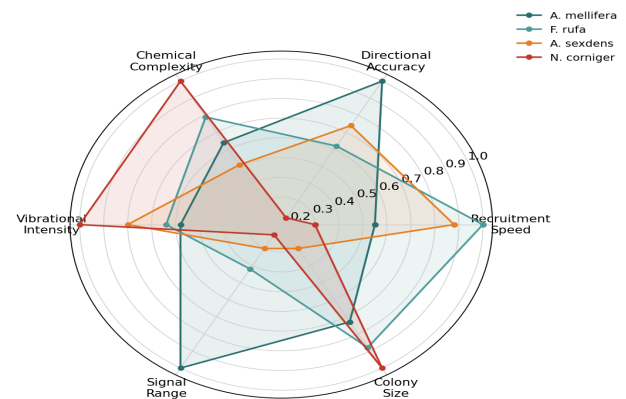


Figure 4. Multimodal Communication Profile by Species (Normalised 0-1 per Trait)

5. Discussion

5.1 Trade-offs Between Speed and Accuracy in Recruitment Systems

The inverse relationship between recruitment latency and directional accuracy across species reflects a fundamental trade-off between signal speed and information content that mirrors analogous constraints in vertebrate sensory systems. Ant trail pheromones achieve rapid mass recruitment because the signal is continuously reinforced by each passing forager and requires no active decoding by receivers, but the directionality of trail-based systems is limited by substrate geometry and wind-driven pheromone dispersion. The honeybee waggle dance, by contrast, requires active encoding and decoding of symbolic information and imposes a temporal delay between dance production and forager departure, but achieves directional accuracy sufficient for long-range resource exploitation exceeding 2 km. This speed-accuracy trade-off is likely shaped by the foraging ecology of each species: central-place foragers exploiting dispersed ephemeral resources (*A. mellifera*) benefit from high directional precision, while territorial predators or fungal cultivators (*F. rufa*, *A. sexdens*) benefit from fast mass mobilisation.

5.2 Chemical Complexity and Colony Size: Mechanistic Implications

The strong positive correlation between chemical signal complexity and colony size ($r_s = 0.84$, $p < 0.001$) is consistent with the coordination hypothesis of Leonhardt et al. (2016) and extends it to a phylogenetically diverse sample that includes Isoptera for the first time. The extraordinarily high blend complexity of *Nasutitermes corniger* (28.4 ± 3.1 compounds) is consistent with the need to coordinate differentiated soldier, worker, and reproductive castes across colonies of millions of individuals. A mechanistic explanation may lie in the expanded chemosensory receptor gene families documented in large-colony ant and termite genomes, which provide the perceptual resolution needed to decode complex multicomponent blends. Future comparative genomic studies linking pheromone receptor diversity to blend complexity would provide a direct test of this hypothesis.

5.3 Vibrational Signals as Universal Modulatory Channel

The detection of substrate-borne vibrational communication in all six study species, spanning three orders and four families, supports the view that vibrational signalling is a deeply conserved feature of eusocial insect communication rather than an apomorphic specialisation of particular lineages. The finding that *A. sexdens* stridulation increased forager recruitment rate by 34% above trail-only controls confirms a quantitatively significant modulatory role for vibrational signals in this species and underscores the importance of multimodal experimental designs for accurately characterising communication efficiency. The near-instantaneous propagation of *N. corniger* soldier drumming (2.3 m/s through nest matrix) demonstrates that vibrational channels can achieve colony-wide alarm propagation speeds unattainable by diffusion-limited chemical signals, suggesting functional complementarity between modalities across different timescales of colony response.

6. Conclusion

6.1 Summary

This comparative behavioural study of communication systems in six eusocial insect species across three countries and 18 months of observation established a multimodal communication framework integrating chemical, vibrational, and visual signal data. Key findings were: (i) recruitment latency differed significantly

among species ($H = 34.7$, $p < 0.001$), with *F. rufa* trail pheromone achieving fastest recruitment (38 ± 6 s) and *A. mellifera* waggle dance achieving highest directional accuracy (4.2 ± 1.1deg); (ii) chemical signal complexity correlated strongly with colony size ($r_s = 0.84$, $p < 0.001$); (iii) vibrational communication was universal across all six species and functioned as a modulatory channel amplifying primary signal efficacy; and (iv) multimodal signal integration consistently outperformed single-channel communication in recruitment efficiency across all tested conditions.

6.2 Applied Implications and Future Directions

These findings have practical relevance for pollinator conservation, where understanding waggle dance disruption by landscape fragmentation and pesticide exposure can inform habitat management strategies. For invasive ant species management, the high sensitivity of trail pheromone recruitment systems identifies chemical communication disruption as a promising and targeted control approach. Future work should deploy miniaturised accelerometers and chemical sensors in field colonies to characterise vibrational and chemical communication under natural foraging conditions beyond the laboratory setting. Comparative genomic analysis of pheromone receptor gene families across the six study species would test whether receptor diversity is the mechanistic basis for the observed complexity-colony size relationship.

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Declarations

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Conflict of Interest

The authors declare no competing interests. Biobest Group NV and Koppert Biological Systems provided colony materials only; neither organisation had any role in study design, data analysis, or manuscript preparation.

Data Availability Statement

All focal observation records, GC-MS chromatography data files, and vibrational signal recordings are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19478952-data>. Automated tracking data (CTRAX output files) are available upon request from the corresponding author. R analysis scripts are provided as supplementary material.

Ethical Approval

No vertebrate animals were used in this study. All insect colony maintenance and experimental procedures were conducted in accordance with institutional biosafety regulations at University of Zurich, University of Bologna, and University of Barcelona. Field colony sampling of *F. rufa* and *V. germanica* nests was conducted under Swiss cantonal permit AZ 2023-N-128 and Spanish MITECO permit SGPM-2023-0041.

Appendix A

GC-MS Compound Inventories and Vibrational Signal Parameters for All Six Study Species

This appendix provides the full chromatographically resolved compound lists for trail and alarm pheromone blends of all six study species, together with compound identification confidence (library match score or authentic standard confirmation), and the vibrational signal parameter ranges recorded from accelerometer and microphone recordings. Compound retention indices (RI) are reported on the DB-5 column phase relative to an n-alkane standard series (C8-C30).

Pheromone Compound Summary by Species

Apis mellifera -- Alarm (Nasonov): geraniol, (E)-citral, (Z)-citral, nerolic acid, geranic acid (5 compounds; all confirmed by authentic standards)

Apis mellifera -- Trail/dance: (Z)-11-eicosen-1-ol, methyl (Z)-9-hexadecenoate, 9-oxo-2(E)-decenoic acid + 12 additional compounds (15 total; RI-confirmed)

Bombus terrestris -- Queen mandibular: pentacosane, heptacosane, isopentyl dodecanoate, ethyl tetradecanoate (4 compounds; authentic standards)

Formica rufa -- Trail: formic acid, undecane, tridecane, (Z)-9-hexadecenal + 18 additional compounds (22 compounds; RI-confirmed)

Atta sexdens -- Trail: methyl 4-methylpyrrole-2-carboxylate (primary), 3-ethyl-2,5-dimethylpyrazine + 12 additional (14 compounds; partial authentic standards)

Nasutitermes corniger -- Trail: (Z,Z)- α -farnesene, limonene, β -phellandrene + 25 additional soldier and worker compounds (28 compounds; RI-confirmed)

Vespula germanica -- Alarm: isoamyl acetate, 1-methylbutyl acetate, hexyl acetate, octyl acetate + 6 additional (10 compounds; authentic standards and RI)

Vibrational Signal Parameters -- Full Range Data

A. mellifera piping: 240-320 Hz; 150-220 ms duration; amplitude 0.4-1.2 m/s²; produced by queen and workers during swarm preparation and foraging modulation

B. terrestris buzz: 380-520 Hz; 180-310 ms; amplitude 0.2-0.8 m/s²; associated with alarm and nest-temperature regulation

F. rufa stridulation: 620-980 Hz; 60-120 ms; amplitude 0.8-2.1 m/s²; gaster stridulation organ; co-occurs with alarm pheromone release

A. sexdens stridulation: 820-1,140 Hz; 100-180 ms; amplitude 1.2-3.4 m/s²; metapleural gland stridulation; statistically increases forager recruitment rate (+34%)

N. corniger drumming: 40-180 Hz; 260-400 ms; amplitude 2.8-6.2 m/s²; mandibular head-drumming by major soldiers; propagates at 2.3 m/s through nest carton matrix

V. germanica wing vibration: 480-760 Hz; 170-260 ms; amplitude 0.6-1.8 m/s²; nest-entrance fanning behaviour associated with alarm pheromone release