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REVIEW ARTICLE

Architecture of the insect society: comparative analysis of collective construction and social function of nests

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Abstract

Many social insects construct nests, which are fundamentally important to the success and survival of the colony. We review recent work on understanding the construction and function of social insect nests and attempt to identify general principles of collective construction and nest architecture in insect societies. We look across taxa, including termites, ants, social bees, and social wasps, specifically focusing on experimental studies that have elucidated the mechanisms by which insect nests are successfully built. We find that selecting materials and nest sites are crucial decisions made by social insects that impact both the resulting nest architecture and colony survival. Social insects utilize cohesive, malleable material to build nests. Often, nests are constructed in a modular manner, allowing social insects to exploit a variety of materials while growing to accommodate population explosions from a few individuals to millions. We note that the regulatory principles that coordinate building behaviors are consistent across taxa. Specifically, encounter rate, positive and negative feedback cycles, stigmergy, and genetic influence all govern the actions of multiple builders and result in a cohesive, functional structure. We further consider empirical studies that demonstrate how nests impact collective behaviors and help insect societies flourish. We find that all social insect nests serve the same key functions: to protect residents and to offer a means of organizing their collective behaviors. Ultimately, we expand our analysis to experiments utilizing robot models of societies, which aim to uncover unifying themes of construction and space use by collectives. Overall, we show that social insect nests represent engineering and construction marvels that provide fundamental insights into how biological collectives succeed in the natural environment, and we suggest that the use of robotic models may provide insight into these fascinating behaviors and structures.

Keywords Dynamical systems · Eusocial · Hymenoptera · Isoptera · Nest · Robotics · Robophysics · Stigmergy

Introduction

Social insects dominate ecosystems. A key factor in the extreme ecological and evolutionary success of social insects is the nest (Korb 2009). Nests extend the body of the social insect "superorganism" and provide protection and hospitable environments for storing food and rearing young (Hansell 2005; Laidre 2021). The structure of the nest promotes division of labor among individuals and influences the social behaviors that define social insect colonies (Tschinkel 2015). As such, understanding social insect nests is paramount to understanding social insects in general.

The behaviors used by social insects to construct nests are remarkable (Buhl et al. 2006; Gordon 2019; Hansell 2005; Invernizzi and Ruxton 2019; Perna and Theraulaz 2017; Theraulaz et al. 2003). Construction of social insect nests occurs through many small coordinated actions of multiple individuals. The physical environment also has a great impact on social insect nests. For example, the structure and function of social insect nests depend heavily on the building materials. Social insects use diverse materials to build nests, such as soil, sand, secretions, leaves, twigs, wood, plant fiber, mud, and wax (Shanahan and Spivak 2021; Harman 2021; Hepburn et al. 2014; Jost 2021; Wenzel 2020). Materials may also convey information in differing ways, such as by maintaining shape, allowing for the diffusion of pheromones, transferring vibrations, or capturing colony

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hydrocarbons and other scent molecules (Hager and Kirchner 2013; Oberst et al. 2020; Post and Jeanne 1981).

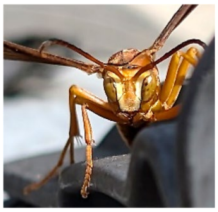
The purpose of this review is to provide a recent update on our understanding of nest construction and function in social insects. This review differs from prior discussions (Perna and Theraulaz 2017; Tschinkel 2015) in that it incorporates all of the ‘traditional’ social insects, including ants and termites, which have been subject to considerable study of nest building, as well as social wasps and bees, which have been subject to fewer investigations of nest construction. By combining information from these disparate taxa, we hope to gain a greater appreciation of the divergent strategies employed by social species to build nests, and pull out universal themes of collective construction and space use. We specifically focus on studies that take an experimental approach to understanding the structure and function of nests. Experimental approaches are particularly useful in helping understand the proximate mechanisms of nest building behavior and the functions of nest structures. In addition, experimental approaches highlight constraints of the physical environment and the importance of materials used to build nests. Thus, this review’s focus on experimental work may further provide pathways for future investigations into understanding social insect nest structure and function.

In addition, we look to the future of investigations and discuss how robophysical experiments can provide novel insight into nest building and function. Robophysical modeling utilizes physical robots as models of animal behavior (Aguilar et al. 2016). Though this incipient field has previously been held back by financial, technical, and cross-disciplinary cultural constraints, we believe that robophysical models have significant potential to capture the impact of physical constraints on behavior and, therefore, highlight certain governing principles. These robophysical studies also have parallels to standard empirical studies of biological systems and can provide different types of insights into social behavior and nest function. It is our hope that this introduction may inspire more biologists to embark on fruitful collaborations employing robophysics to answer biological questions of social insect nest construction and function.

Overview of nest structures across social insects

Highly social insects, which include termites, ants, social bees, and social wasps, build nests (Table 1). Termite nest construction is characterized by excavation and stacking of

Table 1 Traits of social insect taxa and their nests

Trait	 Ants	 Termites	 Social Bees	 Social Wasps
Colony size	Dozens to millions	Dozens to millions	Few to thousands	Few to thousands
Factors influencing nest site selection	Temperature, sunlight, airflow, soil composition	Temperature, humidity, soil composition	Cavity size, temperature, resource availability	Temperature, precipitation, predation
Nest site selector	Single queen or whole colony	Queen and king or whole colony	Single queen or whole colony	Single queen or whole colony
Nest material	Mostly found	Mixture of found and self-made material	Mostly self-made wax	Mostly found, wood pulp
Nest building behaviors	Excavation or construction	Excavation or construction	Mostly construction	Mostly construction
Supported regulatory mechanisms	Local environmental cues, stigmergy, genetic variation, feedback cues	Local environmental cues, stigmergy	Local environmental cues, stigmergy	Local environmental cues, stigmergy, innate rules, genetic variation, feedback cues
Protection provided by nest	Insulation, pathogen defense, predator defense	Insulation, pathogen defense, predator defense	Insulation, predator defense	Insulation, pathogen defense, predator defense
Nest guarding	Behavioral and morphological	Behavioral and morphological	Behavioral	Behavioral
Collective behaviors regulated by nest	Foraging, division of labor	Foraging, movement speed, nestmate encounters, division of labor	Nestmate encounters	Nestmate encounters

excavated materials (Fig. 1A). Termites build both subterranean and above-ground nests (Fig. 1). Many termite species nest directly in the materials they eat (Fig. 1B); however, other species construct homes out of nonbiological material and must leave the nest to forage. The above-ground nests of some termite taxa are massive charismatic structures that jut out above the landscape (Fig. 1C), while others can be more inconspicuous (Fig. 1D). Termite nest structure is fundamentally linked to the materials used for construction (Benedito de Souza 2020; Fruett et al. 2023). In general, the building materials termites use lead to the construction of remarkably durable nests (Francis et al. 2024). Termite nests consist of a variety of structures, including chambers, tunnels, and external shelter tubes. These shelter tubes connect the nests to food sources and sometimes serve as a means of communication through vibrational cues (Hager and Kirchner 2013). Often, termite nests are large, but have a centrally located 'royal chamber', wherein queens and kings reside (Darlington 1985; Tasaki et al. 2020); it is thus very difficult for predators to make their way to the critically important reproductives (Tasaki et al. 2021). Moreover, empirical studies have found that the central chamber has optimal O_2 and CO_2 levels allowing for peak fecundity (Tasaki et al. 2020).

Ants also build or inhabit physical structures that act as nests. Ant nests are used to house and protect brood and adults (Fig. 2A, B), and may also be used to store food. Like termites, ants construct a diversity of nests, from tiny tunnels built within the walls of an acorn, to massive structures stretching several feet underground (Fig. 2C). Some ants even construct nests from live plant material (Fig. 2D). Ants vary greatly in their manipulation of the environment.

Fig. 1 Termite nests and construction. **A** *Reticulitermes flavipes* workers transporting soil for nest construction. Photocredit: creative commons license CC0. **B** *Reticulitermes sp*. constructing an opportunistic nest in old papers. **C** Cathedral Termite (*Nasutitermes triodiae*) mound in Australia. Photocredit: creative commons license CC0. **D** *Nasutitermes walkeri* nest constructed in a tree. Photocredit: creative commons license CC0

Fig. 2 Ant nests and building behaviors. **A** *Solenopsis invicta* fire ants excavating a tunnel for a nest in an artificial glass bead substrate. Photocredit: Daria Monaenkova, Nick Gravish, Greggory Rodriguez. **B** Northern fungus-farming ant *Trachymyrmex septentrionalis* during underground nest construction. **C** *Solenopsis invicta* fire ant mound bisected to show galleries and tunnels within. **D** Weaver ants (*Oecophylla smaragdina*) build arboreal nest chambers constructed from silk and leaves. Photocredit: creative commons license CC0

Some species change very little of their surroundings and nest in preformed cracks in rocks, modifying only the entrance, while others create immense dwellings to house millions of nestmates (Holldobler and Wilson 1990). Similar to termites, ants typically build nests via excavation; however, unlike many termites, ants are not known to nest within material they eat. Once built, the structure of ant nests affects crucial colony-level tasks, such as foraging (Lehue et al. 2020), defense (Donaldson-Matasci et al. 2022), and development (Carlson and Gentry 1973; Cassill et al. 2002; Karlik et al. 2016; Penick and Tschinkel 2008).

Bees exhibit a large variety of nest structures, from simple tubes to complex hives (Fig. 3). Just like ant and termite nests, the primary function of a bee nest is to store and protect brood, adult reproductives, and food. However, unlike termites and ants, many bees construct nests from wax, a self-produced biological material. Moreover, all corbiculate bees use brood cells as the basic unit of the nest; in some cases the nest is little more than one cell, but in other cases nests combine thousands of cells connected via intricate combs (Oldroyd and Pratt 2015). Honeybees in particular are known to arrange wax into hexagons, making optimal use of space for the least amount of wax (Weaire and Phelan 1994; Gallo and Chittka 2018; Pirk et al. 2004). Recent studies using video observations and thermographic sensing demonstrated that worker honeybees actively manipulate wax into hexagonal shape using their antennae, mandibles, and legs in a regular sequence (Bauer and Bienefeld 2013; Nazzi 2016). However, not all bees build neat hexagonal brood cells; bumblebees, for example, construct underground nests with brood cells as well as wax honeypots arranged in a seemingly haphazard manner (Fig. 3). Many bees, including honeybees and stingless bees, are cavity nesters, building nests of a predetermined size in an existing cavity, which contrasts with the majority of ant and termite's nests, which are unbounded.

Social wasp nests are used to rear developing offspring but not to store food, in contrast to the nests of other social

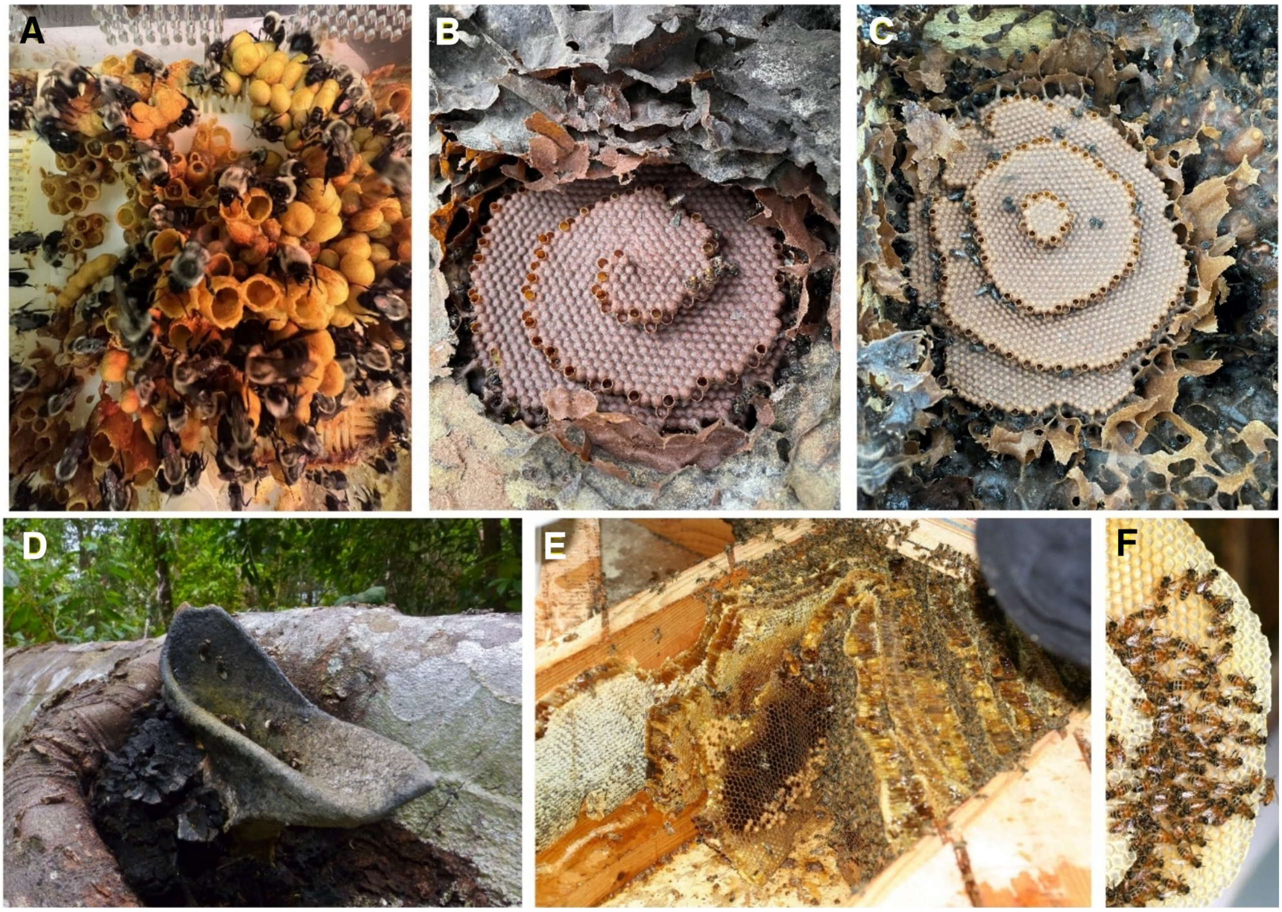


Fig. 3 Bees construct a diversity of nests. **A** Bumblebee (*Bombus impatiens*) nest constructed in a laboratory setting. Photocredit: Sarah Orr. **B** Helicoidal nest comb constructed by *Scaptotrigona depilis* stingless bees. Photocredit: Viviana Di Pietro (Schaerf 2024). **C** Parallel comb constructed by *Scaptotrigona depilis* stingless bees. Photocredit: Viviana Di Pietro (Schaerf 2024). **D** Nest entrance to *Tetrigona binghami* stingless bee nest. Photocredit: creative commons license CC0. **E** Honeybee (*Apis mellifera*) parallel nest combs filling an open cavity in a house floor. **F** Honeybee brood cells and workers

insect taxa. Some wasps build aerial nests suspended from trees or buildings (Fig. 4A, B). Other species nest underground (Fig. 4C, D). Social wasp nests typically consist of multiple layers of hexagonal cells arranged in a distinctive pattern, with each cell serving a specific function such as housing larvae (Fig. 4A, D). The queen, and then the workers, first create the paper-like pulp from chewed wood and saliva, then fashion it into hexagonal cells. The nest grows in size and complexity as more workers join the building effort, with multiple layers of combs constructed over time. Some species build unenclosed nests consisting of a flat sheet of pulp covered in cells (Fig. 4A). This flat sheet is connected to an existing structure, such as a tree or building, with a small stalk of pulp called a petiole. Other wasp species build nests of multiple layers and enclose their nest in paper (Fig. 4C, D). Wasp nest features can also function in colony identity; for example, *Polistes metricus* nest paper hydrocarbons contribute to nestmate recognition (Singer and Espelie 1992). This is a unique property of a wasp nest that has not yet been directly supported in other social insect taxa.

Social insect nest construction

Nest site selection

All social insects must begin nest construction by first selecting a location for their nest. Social insects consider temperature (Jeanne and Morgan 1992), sunlight (Carlson and Gentry 1973; Jeanne and Morgan 1992), precipitation, predation (London and Jeanne 2000), resource proximity (Lanan et al. 2011; Suzuki et al. 2007), and substrate (Aleksiev et al. 2007) as factors when deciding where to build a nest. In addition, certain species take into account special criteria. For example, some arboreal ants rely on the presence of galls when selecting nests (Giannetti et al. 2024). Honeybees select a nest site based on the availability of a

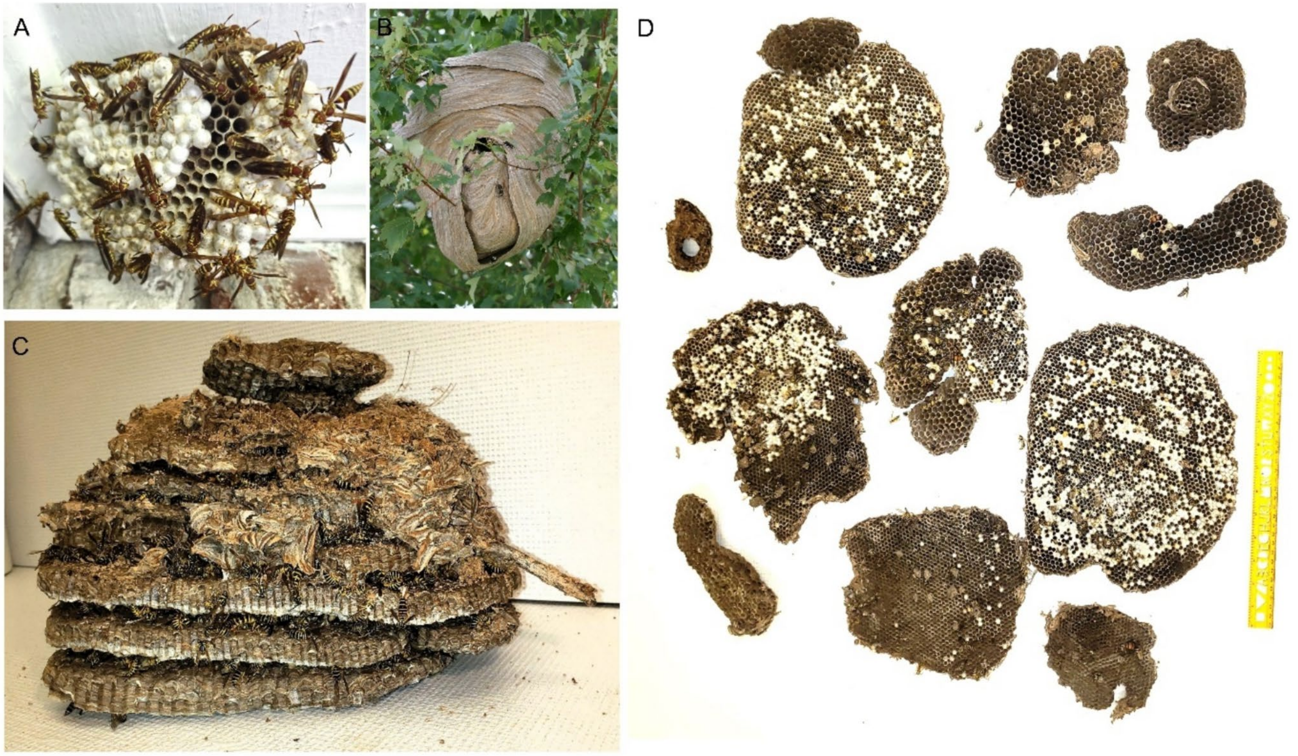


Fig. 4 Nests of vespid social wasps are typically constructed of wood pulp. **A** *Polistes exclamans* builds an open, unenclosed nest. **B** *Dolichovespula maculata* nest enclosed in paper. **C** *Vespula squamosa* nest excavated from the ground with paper removed. **D** Same *V. sqamosa* nest as in (**C**) but combs have been separated. Note the paper around the single entrance hole in the upper left corner and the presence of queen comb, which is used to rear new queens, and has larger cells than worker comb

suitable cavity. Some stingless bee species nest in a diversity of locations (Rachmawati et al. 2022), whereas others show distinct preferences for particular host plants (Macedo et al. 2021). Conversely, bumblebees (*Bombus sp.*) are generalists with respect to their nesting habitats, and are found in underground nests in agricultural, alpine, dune, forest, grassland, and urban landscapes (Liczner and Colla 2019) that are nearby floral resources (Goulson et al. 2010; O'Connor et al. 2017; Suzuki et al. 2007). Many social wasps find suitable nesting locations in human-made structures, such as the eaves or attics of houses (Wenzel 2020). Overall, each species occupies a different ecological niche, and thus has a different definition for the ideal nest site and structure.

Many social insect species display coordinated collective decision-making when it comes to nest site selection (Table 1). For example, experiments in *Temnothorax* revealed coordinated decision-making skills when deciding to relocate to new nests (DiRienzo and Dornhaus 2017; Pratt 2005a; Sasaki et al. 2021). In the case of swarming bees, such as *Apis mellifera* and *A. florea,* a new nest site was selected through a multi-day process, wherein scouts reported on quality and location of potential nest locations (Oldroyd et al. 2008; Seeley and Kirk Visscher 2004). In some cases, scouts even defend attractive nest sites from other colonies (Rangel et al. 2010). Conversely, the construction of a new social wasp nest typically begins with a solitary queen selecting a suitable site, often in a sheltered location, such as a hollow tree or underground burrow (MacDonald and Matthews 1981). To find an optimal nest site, social insects rely on either collective or individual decision-making processes, and each species must weigh different parameters when selecting a suitable location. In general, considerable research has been conducted into the mechanisms by which ants and social bees choose nesting locations, whereas fewer studies have focused on nest site selection in termites and social wasps.

Nest construction materials

Nest construction materials vary within and between taxa, and affect building behaviors and nest architecture. Ants and termites tend to construct nests from granular media arranged into tunnels and chambers, whereas bees and wasps usually construct nests from manipulated biological material arranged into cells (Table 1). Termites build nests from a variety of materials, including soil, mud, wood, saliva, and feces (Noirot and Darlington 2000; Ptáček et al. 2013) (Fig. 1A, B). Ants also encounter many kinds of building materials in their environments, such as soil, rocks, leaves, twigs, and other plant materials (Bruce et al. 2019; Diehl-Fleig and Diehl 2007; Forti et al. 2007; Tschinkel 2004) (Fig. 2C, D). However, both ants and termites mainly construct nests by excavating cohesive granular material. Excavation brings the risk of tunnel or chamber collapses, and requires ant and termite nests to be structurally sound enough to bear the weight of the soil forming the roof of their homes (Mikheyev and Tschinkel 2004).

Termite building activities and resulting structures are affected by soil texture and water concentration; termites prefer to dig in moist (Arab and Costa-Leonardo 2005; Facchini et al. 2023; Green et al. 2005; Houseman and Gold 2003; Su and Puche 2003), homogenous (Arab and Costa-Leonardo 2005) substrates. Similarly, *Solenopsis invicta* fire ant colonies, which nest in soil, display dramatic differences in nest structure depending on the moisture content of soils, with the deepest tunnels being achieved in material with intermediate moisture content (Monaenkova et al. 2015). *S. invicta* ants also excavate grains of multiple sizes (Monaenkova et al. 2015). Experimental work in *Temnothorax albipennis* has also demonstrated a preference for grains of varied sizes, the use of which may increase the resilience of the resulting nest (Aleksiev et al. 2007). It remains unclear whether these preferences arise from an inherent advantage to homogeneous or heterogeneous materials, or whether it is a product of each taxon's evolutionary history.

Soil composition is also important to nest construction. For example, a comparison of the nests of the fungus-growing termite *Odontotermes obesus* in two forests with different soil compositions found that mound complexity was affected by clay content (Jouquet et al. 2015). Clay content also contributes to the structural stability of termite mounds in *Macrotermes bellicosus* (Jouquet et al. 2004) and *Coptotermes acinaciformis*. Specifically, *C. acinaciformis* uses clay to reinforce load-bearing wood within the nest, which allows colony members to eat the previously load-bearing wood itself (Oberst et al. 2016). Moreover, a field study found that the materials composing shelter tubes dictated the tubes' water resistance and effectiveness. In particular, *Coptotermes formosanus* and *Nasutitermes takasagoensis* termites utilize soil, fluid secretions, and feces to construct highly water-resistant shelter tubes, while *Odontotermes formosanus,* which likely conserves feces for fungus-growing, constructs less water-resistant shelter tubes out of soil and fluid secretion alone (Chiu et al. 2022). While similar studies testing the effects of differing soil compositions on nest architecture and function have yet to be performed in ants, it is well-established that the soil within ant nests is chemically different from surrounding soils (Farji-Brener and Werenkraut 2017; Frouz et al. 2003; Wagner et al. 1997, 2004). However, it remains unclear if this is due to soil selection by the ants, or, perhaps more likely, a side effect of foraging, waste production, and soil mixing via excavation. Thus, future investigations of the soil composition in ant nests could be fruitful.

Social bees and wasps often produce nests from substrates that are created by combining foraged materials with biological secretions (Table 1). Many bees build nests from wax, which is a mixture of fatty acids, esters, and hydrocarbons (Blomquist et al. 1980; Hepburn et al. 2014). Each worker bee has wax glands, wherein the sugar from honey is converted to wax. Wax production varies with age, with 9-day-old bees producing the most wax (Hepburn et al. 1991). Freshly produced wax is chewed to become malleable enough to form brood cells (Casteel 1912; Kurstjens et al. 1985), which sometimes incorporate other materials, including plant fibers, resin, mud, stones, or animal fur. Wasp cells look very similar to those built by honeybees, although they represent independent origins of cell architecture. However, wasps' nests are typically built from paper, created by chewing wood pulp, rather than from wax. This convergent evolution of a hexagonal cell architecture perhaps belies the theory that the hexagonal cells of a honeybee comb are the result of a liquid equilibrium process (Pirk et al. 2004; Talukdar and Dutta 2019), aligning more with findings that bees engage in direct construction (Bauer and Bienefeld 2013). Wax composition is important to the physical properties of a bee nest (Buchwald et al. 2009). Likewise, the protein concentration of the paper used to build a paper wasp nest affects waterproofing and durability (Curtis et al. 2005). However, wasps (Orr and Parker 2023) and bees (Allasino et al. 2019; MacIvor and Moore 2013) have both recently been found to construct nests from plastic, suggesting these taxa have an innate flexibility in nesting materials (Albacete et al. 2024).

In summary, the different physical materials used by distinct social insect taxa each offer certain advantages and impose different constraints. This results in a myriad of divergent construction behaviors unique to each media. For example, termites and many ants tend to excavate the material already present in their nest, while wasps, some bees, and some ants forage for specific construction materials to bring to the nest sites. However, all the media utilized by social insects to construct nests is both malleable and cohesive, but also ultimately firm and structurally sound. Across taxa, the specific composition of media impacts the function of the nest and each taxon has its own way of controlling that media composition: behaviorally in the case of ants and termites, and physiologically in the case of bees and wasps. Interestingly, bee and wasp nests have been shown to remain robust in the face of non-optimal media; future work might experimentally compare the nests of bees and wasps constructed from traditional and alternative materials, akin to experiments varying substrate density in ants and termites.

Nest construction behaviors

Construction behaviors across social insect taxa are impressive, effective, and robust. For example, experiments have demonstrated that honeybee comb geometry is not significantly different when constructed in zero gravity (Vandenberg et al. 1985). Honeybees will even cooperate to build functional cells in mixed-species colonies of *A. mellifera* and *A. cerana*, despite differences in wax chemical makeup, cell size, and construction behavior (Yang et al. 2010). Likewise, termites and ants will excavate nest tunnels in a variety of substrates (Arab and Costa-Leonardo 2005; Green et al. 2005; Houseman and Gold 2003; Monaenkova et al. 2015). Relatively less is known about the effectiveness of social wasp construction behaviors in the face of similar perturbations, though, as noted above, social wasps have been found capable of constructing nests with non-traditional substrates (Albacete et al. 2024; Orr and Parker 2023).

Social insects utilize a variety of behaviors to build nests. Ants and termites, in particular, construct nests through excavation and deposition of materials, and must physically excavate and remove the full volume of their nest (Table 1). For example, workers of the termites *Heterotermes aureus* and *Gnathamitermes perplexus* transport sand particles with their mandibles, while *Paraneotermes simplicicornis* workers excavate with their legs, kicking sand backward (Bardunias and Su 2010). *Solenopsis invicta* ant workers modify their behaviors depending on soil composition. Workers tend to grasp single particles in coarse substrates, but actively form pellets of fine substrates by raking mandibles and forelimbs across the substrate to gather many small particles together into a pellet (Monaenkova et al. 2015). Thus, though termites and ants both generally engage in excavation, the specific mechanisms by which they do so varies.

Tunnels within nests tend to be thinnest at the expanding construction front, resulting in crowding at the areas of highest construction activity. In response, termites may form queues when excavating within a nest (Bardunias and Su 2010). Laboratory experiments have demonstrated important differences in how termites transport excavated material, and in what they do when approaching one of these queues. For example, *P. simplicicornis* utilizes a "bucket brigade" strategy to remove excavated material. In contrast, *H. aureus* and *Reticulitermes tibialis* individuals transport material individually. Despite these behavioral differences, *P. simplicicornis* nests parallel *H. aureus* nests in complexity, which demonstrates that different building behaviors can lead to similar nest structure. In contrast, *R. tibialis* is the architectural outlier of the three species, with the least complex nests. The structural differences arise from a single behavioral difference related to the decision to wait in the queue or excavate further (Mizumoto et al. 2020). Thus, tuning a single action can result in large differences in nest architecture between species. In particular, this case study in termites demonstrates how physical constraints pose a challenge that can be met in a variety of ways, with the varied responses having distinct architectural consequences. Interestingly, despite similar constraints, ants do not form queues during excavation, potentially due to crowding avoidance mechanisms (Czaczkes et al. 2013).

Nests grow as the colony grows. Therefore, excavation of an ant or termite nest, and construction of a bee or wasp nest, is rarely complete. This is true across taxa, with the total volume of an ant (Mikheyev and Tschinkel 2004; Rasse and Deneubourg 2001), termite (Lima Pequeno et al. 2013), bee, or wasp (Grinsted and Field 2018) nest increasing with population size. In particular, many social wasp species continuously expand nests throughout the season (Eberhard 1969; Marino Piccioli and Pardi 1978), though some cease construction during larval production (Marino Piccioli and Pardi 1978; Miyano 1986). However, swarm-founding wasps typically feature explosive nest construction in which nests are rapidly built during early founding but remain constant in size throughout the season (Jeanne and Bouwma 2004). Likewise, honeybee nests follow a rapid growth process (Marting et al. 2023) characterized by an initial burst reminiscent of this explosive wasp nest construction, except that bee nest construction is followed by pulses of comb growth throughout the season (Pratt 1999). Thus, the biological lifecycle of the organism in part determines the growth pattern of the nest itself.

Honeybee nests grow quickly in part because multiple combs are built in parallel (Marting et al. 2023). During construction, honeybees expand their nests in multiple dimensions equally until combs hit the edge of the cavity, which results in a spheroid-shaped nest (Marting et al. 2023). Conversely, ant nests can grow via the addition or extension of shafts in a modular process, with chambers being formed in the same direction as the tunnels at the entrances of these chambers (Mikheyev and Tschinkel 2004). This modular construction process parallels the modular addition of new combs in a bee nest (Pratt 1999). However, the lack of a defined cavity and the lack of parallel construction results in irregular, asymmetric, often top-heavy nests composed of various protrusions (Mikheyev and Tschinkel 2004; Minter et al. 2012), in contrast to the spheroid honeybee nests. Thus, the growth pattern of the nest contributes to differences in its resultant architecture.

Nests must occasionally be repaired. Experimental manipulations of honeybee nests reveal that bees prioritize repairing connections over nest expansion, although disruption of nest structures does not hinder nest growth (Marting et al. 2023). Likewise, leaf-cutter ants repair damaged nest mounds, utilizing both normal nesting material as well as refuse (Farji-Brener and Tadey 2012). Wasps must forage for additional wood pulp to repair a damaged nest; however, this does not affect foraging activities, because individual foragers specialize on collecting specific materials (O'Donnell and Jeanne 1990). Termite nest repair consists of first closing off the exposed tunnels before actively making repairs (Mathews 1977). Large termite soldiers first arrive at the damaged site but are quickly replaced with smaller workers (Andrade et al. 2024). This type of specialization mirrors that seen in some social wasps (O'Donnell and Jeanne 1990). On the whole, the ubiquity of nest repair underscores the robustness of social insect nest construction, and likely contributes to the ecological success of social insects.

Altogether, social insects utilize a plethora of construction behaviors to manipulate physical materials into nests. Typically, these behaviors are stereotyped within a species, but vary considerably across species. Excavation and deposition are important behaviors for ants and termites, while manipulation of biological material is part of nest construction for bees and wasps. Nests must grow with the colony and can be repaired if damaged. In some social wasps, growth is constant, while in bees and other wasp species, growth is most rapid at the beginning phases of construction. Expanding underground nests bypasses physical limitations imposed by cavity or arboreal nests; thus, species building cavity or arboreal nests may have limitations on colony size. Finally, most social insects must deal with construction in the face of crowding and confined spaces. The effects of crowding have been heavily studied in ants and termites, but have received less attention in bees and wasps, though these taxa are assumed to experience similar constraints. In general, construction behaviors vary widely among taxa and are impacted by the physical characteristics of the nest material as well as the physiological characteristics of the organisms themselves.

Coordinating multiple builders

Many individuals partake in nest construction; thus, the actions of various individuals must be coordinated across time and space. The processes used to organize individual building actions into coherent collective nest construction show similarities among social insect taxa. Building behaviors are decentralized and self-organized. Individuals use information in the environment to successfully build nests. In particular, stigmergic cues, which are environmental signals left by one individual that influence the activity of another, are thought to be fundamentally important in social insect construction behaviors (Avinery et al. 2023; Calovi et al. 2019; Di Pietro et al. 2024; Facchini et al. 2023; Khuong et al. 2016) (Fig. 5, Table 1). No single individual has a conception of how the nest should be built or what it should look like when complete (Korb 2003; Theraulaz et al. 1998). Instead, each individual worker undertakes simple tasks, and uses local cues that provide information for the construction of complex structures (Camazine et al. 2003; Detrain and Deneubourg 2006; Fewell 2003; Invernizzi and Ruxton 2019; Khuong et al. 2016).

Tunnel width and chamber size are important factors regulated by stigmergic cues (Khuong et al. 2016). Ants and termites both excavate particular sized tunnels and chambers and later modify tunnels to achieve preferred dimensions. Some bees also construct tunnels of specific sizes and dimensions (Ostwald et al. 2020). In general, tunnel and chamber sizes tend to be related to the size of the individuals using and constructing the nest.

Construction behaviors are frequently governed by local environmental cues including the shape of a substrate's surface, humidity within the nest, and chemical cues stored in the substrate (Table 1). For example, *M. michaelseni* worker termites used surface curvature as an important building cue (Calovi et al. 2019; Facchini et al. 2023). Likewise, both ants and termites tend to initiate tunnels in premade indentations (Lee et al. 2008a, b). Moreover, both the fungus-farming termite, *O. obesus,* and the leaf-cutter ant, *Acromyrmex ambiguus*, are sensitive to changes in humidity. Humidity levels also affect construction behavior in some ants; in one study, ant workers did not react to humid air blown into the nest, but holes blowing dry air were plugged with vegetation (Bollazzi and Roces 2007). In addition, a laboratory study in *Macrotermes* found that construction was mainly organized by the location of deposition sites; these sites were in turn associated with aggregations of workers, such that excavation sites with higher numbers of workers attracted more workers (Green et al. 2017).

Another empirical investigation, which involved tracking *Macrotermes michaelseni* workers in an arena, showed that termites prefer to interact with soil that has been recently handled by nestmates. These results provide support for a role of chemical cues in regulating construction activities (Petersen et al. 2015). Similarly, the construction of ant nests involves a variety of social cues (Sudd 1972; Pinter-Wollman et al. 2013; Avinery et al. 2023) and is often facilitated by pheromones (Chen and Zhang 2013). Experiments in *Lasius niger* have explored stigmergic interactions between ants and their nests during construction, finding that workers continue building on soil piles containing a nestmate's pheromones and stop building when piles are taller than their body length (Khuong et al. 2016).

Support for the importance of stigmergy in bee nest construction has been uncovered by studying comb-building stingless bees. Strikingly, *Scaptotrigona depilis* combs are connected in one of the two ways: either via a single helix or as separate parallel combs attached to a central column (Fig. 3B, C). A cross-fostering experiment demonstrated that these architectural differences in comb structure develop as a result of stigmergic cues; rather than constructing a nest matching their natal nest, workers instead continue building

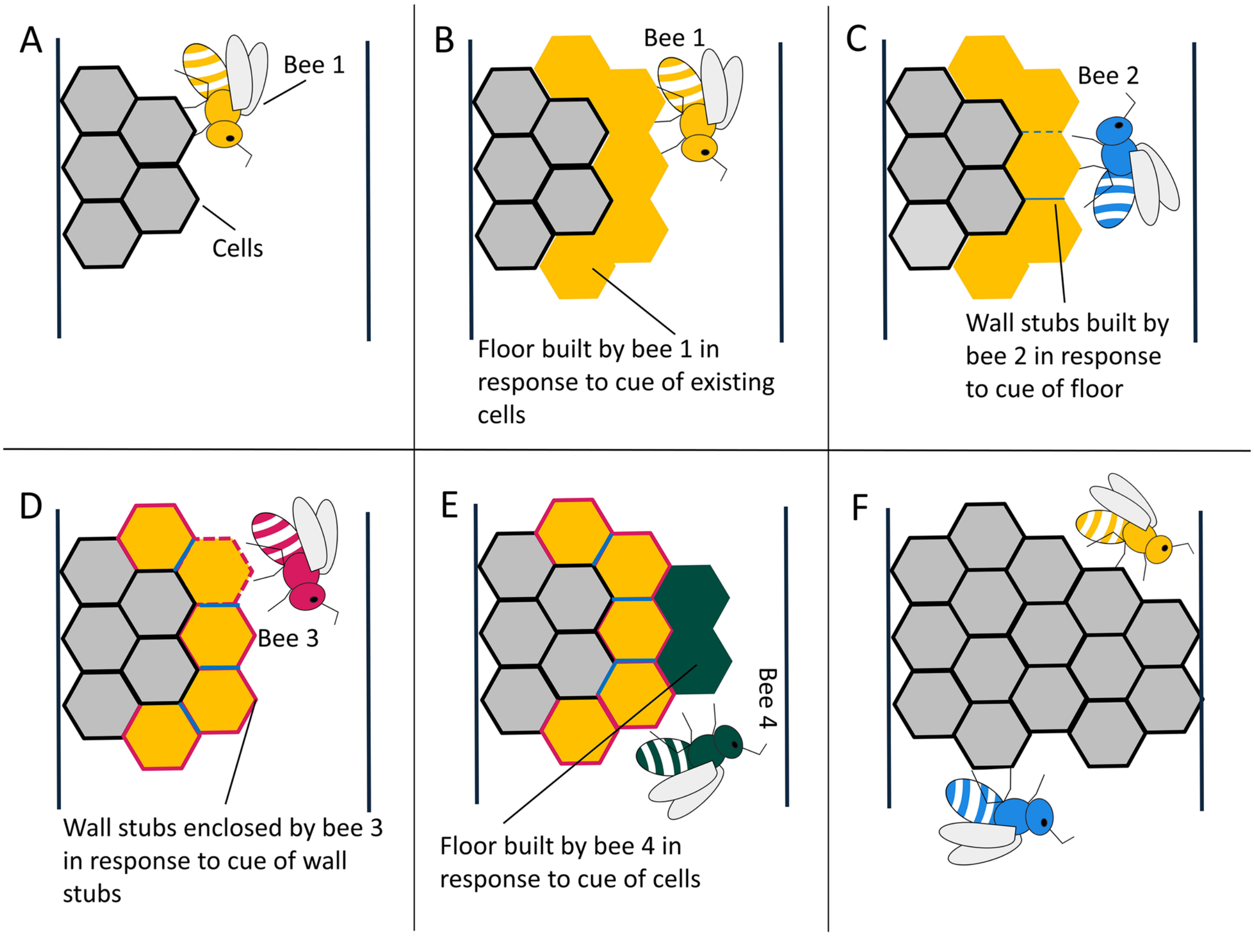


Fig. 5 Cell-building in honeybees exemplifies how stigmergy regulates building behaviors and leads to the construction of nests in insect societies (Nazzi 2016). **A** Bee #1 interacts with cells constructed by her nestmates. **B** Cells act as cues for bee #1 to extend the floor of the nest. **C** Floor acts as a cue for bee #2 to begin constructing stubs of a wall. **D** Third bee detects these wall stubs and responds by adding to the stubs to encircle a cell. **E** Fourth bee notices cells constructed by her nestmates and responds by extending the floor further. **F** After additional building activity by several bees, the comb of cells hits the edge of the cavity. Different colored bees indicate distinct individuals

whichever nest type they were presented with (Di Pietro et al. 2024). Stigmergy also appears to be important to wasp nest construction. Experimental manipulation of nests during construction revealed that both the Eumenid wasp *Paralastor sp.* and the paper wasp *Polistes fuscatus* respond mainly to cues from previous construction rather than correcting changes made by researchers, even when experimental modification makes normal nest architecture impossible (Downing and Jeanne 1988; Smith 1978). Empirical work on *P. fuscatus* further revealed that workers perform a linear sequence of steps during nest construction, relying on existing construction to cue the next phase of building. Overall, these empirical studies demonstrate that topological and chemosensory cues dictate nest construction across social insect taxa, and hint at stigmergy as a regulatory principle coordinating the actions of many builders.

Conversely, *P. fuscatus* wasps repeatedly re-evaluate some nest parameters, such as the distance of the nest to its substrate (Downing and Jeanne 1988). Thus, they appear to use innate rules about overarching architectural parameters to direct construction behavior rather than relying purely on stigmergic cues. Other internal cues may also regulate wasp nest construction. For example, the construction of nests by *Metapolybia* wasps may be governed via their "common stomach" (Karsai and Schmickl 2011). Workers engage in trophallaxis of the water needed for pulp production, which creates positive and negative feedback cycles that regulate behavior (Karsai and Schmickl 2011). In this way, the condition of the colony as a whole regulates collective building behaviors, resulting in a nest that truly represents the extended phenotype of the colony rather than that of any one individual. However, trophallaxis is unlikely to regulate nest construction in soil-dwelling social insects that do not utilize foraged material in nest construction.

Positive and negative behavioral feedback is also thought to be important in nest building activities (Gravish et al. 2013; Karsai and Schmickl 2011; Minter et al. 2012; Monaenkova et al. 2015) (Table 1). Positive feedback regulates many collective behaviors in social insects, including foraging in ants (Aron et al. 1993). Likewise, negative feedback has been found to help ants avoid crowding (Czaczkes et al. 2013) and to regulate foraging in both ants (Robinson et al. 2005) and bees (Borofsky et al. 2020). Thus, these mechanisms may also contribute to collective construction, and can explain excavation dynamics (Minter et al. 2012).

Many previous investigations have suggested that encounter rate may be critical to understanding how social groups interpret and manipulate their environment (Avinery et al. 2023; Davidson and Gordon 2017; Gravish et al. 2013; Modlmeier et al. 2019; Pratt 2005b). The simple act of antennating another ant may provide important information on group size and density (Gordon 2010). The confined space of a nest will affect encounter rates, highlighting the cyclical interplay between stigmergy and behavioral feedback loops.

Finally, genetic variation can also influence nest construction (Table 1). Genetic differences between ant colonies are correlated with variation in nest structure. Experiments in *Temnothorax rugatulus* ants discovered that variation in nest building is more dependent on the inherent behavior of the individual colony than on environmental variation arising from differences in humidity and airflow (DiRienzo and Dornhaus 2017). Similarly, experiments in two species of *Pogonomyrmex* harvester ants further supported the hypothesis that environmental conditions do not strongly influence overall nest shape, suggesting that phenotypic variation between nests arises from genetic differences affecting nest construction (O'Fallon et al. 2022). Strikingly, nest architecture can even be modified at the colony level by the contribution of a single patriline (Schlüns et al. 2011). Moreover, one investigation of *Polistes fuscatus* wasps found that individuals repeatedly built petioles of the same length, suggesting each individual has a set threshold length which functions as the cue to begin construction of the first nest sheet, but that this threshold varies among individuals (Downing and Jeanne 1988). Though this study did not implicate genotype as the source of this variation, genetic differences are a likely source of repeatable individual variation. Thus, genetic variation contributes to behavioral variation in construction, which subsequently affects variation in nest structure.

Overall, we find that a variety of factors contribute to the coordination of nest construction. Social insects use decentralized mechanisms to build nests. In particular, stigmergic cues help individuals respond to their environment and make appropriate decisions regarding nest construction. Some species use chemical signals to encourage building activities. Other species use physical cues to indicate areas of construction. Positive feedback loops then lead to the development of nest structures. We also note that there are fewer mechanisms regulating construction behaviors than possible construction behaviors themselves. Thus, a diversity of behaviors is regulated by a sparser number of more conserved coordination mechanisms.

Social insect nest function

Protection

The nest provides protection against environmental threats, resource thieves, and predators, and is a generally insulated location to store resources and rear brood. Nest temperature is an important regulator of insect physiology, and the nests of many species of termites (Zachariah et al. 2020), ants (Smith and Tschinkel 2007), bees (Taylor and Cameron 2003) and wasps (Höcherl et al. 2016; Hozumi and Yamane 2001) enable efficient thermoregulation. For example, the fungus-farming termite *O. obesus* constructs bi-layered nests with dense, structurally strong cores and porous outer layers optimized for ventilation (Zachariah et al. 2020). Ant nests are also often built to reach a thermal optimum for the colony. Experiments have shown that nests of some species are highly influenced by the presence of direct sunlight, which warms the nest and the colony. Colonies of many taxa will move nests from shaded areas to sunny areas if needed (Carlson and Gentry 1973) or face their nests toward sunlight (Porter and Tschinkel 1987). Bee nests maintain a thermal equilibrium as well. For example, nests of the Amazonian bumble bee were found to be 4.5 °C warmer than external temperatures, and remained dry despite heavy rainfall (Taylor and Cameron 2003). Likewise, honeybee nests maintain strict thermoregulation through both active and passive processes (Stabentheiner et al. 2010); genetic diversity of workers has even been found to stabilize brood nest temperature (Jones et al. 2004). While the temperature of enclosed wasp nests can be regulated similar to bee, ant, and termite nests, the environs of unenclosed wasp nests may be more difficult to control. Consequently, some wasp species that build unenclosed nests have evolved techniques for moderating temperatures. For example, some *Polistes* species build extra external cells that moderate internal temperatures (Hozumi and Yamane 2001). In addition, the temperatures of unenclosed nests can be altered by modifying the petiole to change the orientation of the cells relative to heat sources (Bouchebti et al. 2023; Höcherl et al. 2016); brood develops faster in sites warmed by the sun than in cooler sites (Jeanne and Morgan 1992). On the whole, thermoregulation is a crucial function of social insect nests across taxa, driven by the physical interactions with the environment, nest material and architecture, as well as individual behavior and physiology.

Nests also provide some protection against pathogens. For instance, the subterranean termite *Coptotermes formosanus* constructs nests using feces, which promotes the growth of actinobacteria that may protect the termites from pathogens (Chouvenc et al. 2013). Likewise, antimicrobial and antibiotic producing bacteria have been isolated from the nests of paper wasps (Madden et al. 2013), and *Lasius niger* ants (Efimenko et al. 2020). In particular, *Azteca* ants have been found to maintain distinct microbiomes across various nest chambers (Lucas et al. 2019). Ants also sanitize nest material with their own antimicrobial secretions (Tranter et al. 2013). Moreover, the multiple compartments of social insect nests provide an organizational framework that separates individuals of different castes, ages, and tasks, reducing pathogen-transmitting interactions (Hart and Ratnieks 2001; Mersch et al. 2013; Stroeymeyt et al. 2018).

Of course, nests must be defended from larger threats as well. Many factors influence the defensibility of an ant nest, including the location of the nest (Hölldobler and Lumsden 1980; Powell 2009), nest size (Couvillon et al. 2008), and nest architecture (Bänziger et al. 2011). However, nest entrances seem to be key features and are often modified and fortified (Bennett and Baudier 2021; Lanan et al. 2011; Powell and Clark 2004). Entrance size and number impacts foraging (Lehue et al. 2020) and evacuation speed (Lehue and Detrain 2019, 2020; Pinter-Wollman et al. 2013; Pless et al. 2015). Some species of *Cephalotes* ants prefer small nest entrances and need only a single soldier caste to block the entrance. However, congeners lacking this soldier caste require multiple individuals to defend nest entrances (Powell 2008) (Table 1). The degree of specialization of the soldier caste has also been shown to influence entrance modifications across *Cephalotes*; species that have the least variable nest entrances tend to have the most specialized soldier castes (Powell 2008, 2009, 2016) (Table 1). This finding has also been uncovered in termites, where soldier morphology is correlated with nest site preference across species (Thompson et al. 2001) (Table 1). Honeybees, bumblebees, and stingless bees also have guards situated at the hive entrance (Blacher et al. 2013; Butler and Free 1952; Couvillon et al. 2008; Free 1958; Stabentheiner et al. 2002; van Zweden et al. 2011) (Table 1). Furthermore, comparative studies on stingless bees (Meliponini) have revealed that nest entrance sizes correlate with foraging and aggressive behaviors; species with greater foraging traffic typically have larger nest entrances, and also tend to have more aggressive guards (Couvillon et al. 2008).

Nest entrances are important even in rock ants (Giannetti et al. 2022) and stingless bees (Bänziger et al. 2011; Couvillon et al. 2008) which do not engage in substantial nest construction. Stingless bees modify their nest entrances in a variety of ways (Fig. 3D). Some entrances promote forager survival. Such is the case for *Partamona helleri*, which builds funnel-shaped nest entrances enabling individuals to “crash land” into nests to evade predation (Shackleton et al. 2019). *Pariotrigona klossi,* on the other hand, builds very narrow and long nest entrance tubes to increase defensibility against predators. Workers even ornament these tubes with branching resin so the tubes blend into the limestone rock faces in which they nest (Bänziger et al. 2011). In addition, a survey of the nest entrances of 58 stingless bee species found that the nest entrances tend to feature stripes, dark centers, and peripheral dots, which promote visual recognition by the bees (Biesmeijer et al. 2005). These nest entrance features likely assist bees in quickly finding their homes, which allows the bees to evade predation and efficiently forage. In addition, at least one species of stingless bee, *Tetragonisca angustula*, closes its nest entrances at night (Bennett and Baudier 2021). Similarly, workers of *Melipona* bees block nest entrances with balls of mud (Kerr 1984) or wax (Nunes et al. 2014). Surprisingly, relatively little attention has been paid to the study of nest entrances in termites.

Many species of social wasps, in contrast to ants and termites, build unenclosed nests that do not feature “entrances.” In these cases, nests often rely on chemical means to dissuade predators. Some *Polistes* species are known to smear their nests with a glandular secretion found to repel ants (Jeanne 1975). In *P. fuscatus*, this repellant is smeared on the petiole, which is the only route for invading ants to access the nest (Post and Jeanne 1981). Typically, independent-founding wasps build exposed nests (Jeanne 1975), relying mainly on chemical defense, whereas swarm-founding species build enclosed nests and utilize active defense; the presence of an envelope restricts nest access to a small entrance area that can be guarded (London and Jeanne 2000).

Nest structure can also meet defensive needs as colonies change; for example, *Temnothorax rugatulus* rock ants build thicker nest walls when they have more brood (DiRienzo and Dornhaus 2017). Likewise, *Cephalotes rohweri* deploy more soldiers when nests are less defensible (Powell et al. 2017). Several ants, such as *Cephalotes sp*. (Priest et al. 2021), *Crematogaster torosa* (Lanan et al. 2011)*, Colobopsis truncata*, and *Temnothorax italicus*, also defend their nests by modifying nest entrances in the face of threats (Giannetti et al. 2022). These findings highlight the everchanging nature of social insect construction and underscore the need for regulation of nest structure such that agents continuously receive information from the environment and respond appropriately.

Overall, nests serve to protect inhabitants from weather, infection, and predation. These functions are critical for the survival of any social insect colony. Across taxa, various physical factors influence nest defensibility, including nest material, wall width, connectivity, and entrance number and size. In addition, the physical defensiveness of the nest is often supplemented with active guards and defensive chemicals, highlighting the importance of defense. The diversity of solutions to colony protection can potentially serve as construction inspiration. Looking across distantly related social insect taxa prompts questions, such as why some wasps have not evolved enclosed nests when such structures apparently offer benefits in other taxa. However, some solutions are relatively common, such as optimizing access to sunlight for maintaining optimal temperatures, relying on distinct microbiota for antimicrobial and antibiotic resistance, and physically blocking or guarding entrances to protect from predators.

Regulation of collective behaviors

Nests are arenas for social activities and influence collective behaviors. The nest must allow for efficient communication and traffic flow. Akin to the body of an organism organizing processes such as digestion, cognition, and reproduction into optimized chambers, the nest scaffolds the body of the superorganism, and must physically arrange foraging, communication, and division of labor into specialized but connected areas. Moreover, nest architecture affects movement and guides individuals in specific ways. Thus, a fundamentally important function of nests is in influencing the organization of behaviors among individuals.

Foraging is a key collective behavior impacted by nest architecture, particularly in ants and termites (Table 1). In fact, foraging strategy better explains variation in ant nest architecture than phylogeny (O'Fallon et al. 2023). Ant nest structure impacts the recruitment rate of foragers (Pless et al. 2015; Vaes et al. 2020). The number of nest entrances strongly influences foraging; more entrances enable exploitation of multiple resources (Lehue et al. 2020; Lehue and Detrain 2020). Perhaps the most extreme case of nest entrances' impact on foraging is found in the ant *Allomerus decemarticulatus*, which relies on platforms dappled in nest entrances to cooperatively ambush large insect prey (Dejean et al. 2005). A field study in the bumblebee *Bombus pullatus* found that individual nest openings were used for either entering or exiting, and that total use varied significantly among entrances (Hines et al. 2007). The width of the nest entrance also influences both foraging behavior and evacuation speed; as expected, wider entrances are correlated with increased foraging rates (Rodríguez-Planes and Farji-Brener 2019), yet wider tunnels decrease evacuation speed under stressed conditions (Bruce et al. 2019). Thus, nests often must be optimized within the context of a tradeoff between defensibility and facilitating efficient foraging.

Many termites nest in the material they eat. In these cases, movement through the nest directly correlates with foraging rate. The surface characteristics of the materials used for building impact termite movement as well (Lee 2018). Experimental studies have revealed that termites hesitate when tunnels become wider (Cho and Lee 2014), but that termites actually prefer wider tunnels when given a choice (Ku et al. 2010, 2012). Tunnel curvature also impacts movement. Increasing curvature predisposes termites to favor one wall when walking, which in turn produces more head-to-head encounters (Ku et al. 2012). Experimental studies have found that termites move quicker through tunnels with rounded rather than sharp corners, and seem to pile material into sharp corners to produce more rounded tunnel features (Lee et al. 2008a, b).

On a more general level, encounters within the nest are affected by tunnel width in termites (Ku et al. 2012) and bees (Gerling et al. 1981), which in turn affects communication and other aspects of collective behavior (Table 1). Just as the width, shape, and connectivity of roads impact human traffic, the width, shape, and connectivity of tunnels within ant nests dictate important features of traffic flow (Aguilar et al. 2018). Bee nest tunnel width also affects dominance interactions. Xylocopine bees prevent one another from passing in a tunnel as a display of dominance (Gerling et al. 1981); however, this behavior relies on tunnels narrow enough for one bee to prevent passage of another (Ostwald et al. 2020).

Nest structure has strong effects on division of labor (Pinter-Wollman et al. 2013, 2017) (Table 1), information transfer (Aguilar et al. 2018; Cruz et al. 1997; Gravish et al. 2013, 2015), and individual physiology (Cassill et al. 2002; Tschinkel 2004). Nests provide separate locations to organize distinct tasks, with reproductives and young typically situated in the interior alongside nurses, while foragers and soldiers are more likely to be found closer to the exterior and entrances (Bennett and Baudier 2021; Kwapich and Tschinkel 2013). In particular, termites exhibit different behaviors based on their location. For example, a termite's distance from egg clusters influences its behavior (Du et al. 2017). This spatial distribution of workers has even been shown to be robust to the removal of an entire age class of worker (Lee et al. 2022).

Altogether, social insect foraging, encounters, dominance, and division of labor are all aspects of collective behavior that are partly regulated by physical features of the nest. This is true across taxa and suggests both the importance of regulating these tasks as well as the nuanced role of nest architecture in governing the collective, coordinated tasks of a social insect colony. Thus, the nest is not merely a space to house termites, ants, bees, or wasps, but rather a functional body that modifies and optimizes concerted group behaviors.

Looking forward: testing hypotheses of social insect nest construction and function with robophysical models

In the following section, we propose "robophysical" modeling as a novel means of testing basic principles of collective construction. Robophysical models inherently incorporate aspects of a messy physical environment, such as friction, entanglement, and confinement, which could be overlooked in in silico models, but which may drastically impact function in the real world. In particular, the cohesive granular media utilized by many social insects is challenging to model in simulated environments; tools such as discrete element methods, or other existing methods for estimating behavior of granular materials, are often computationally prohibitive (Fang et al. 2021; Cundall and Strack 1979). In contrast, granular substrates can be introduced to experimental systems readily. Moreover, robophysical approaches allow for the study multiple discrete agents operating in a social context. Thus, we suggest that robophysical modeling may be informative in understanding social insect nest construction behaviors in the future.

Existing robotics approaches

Current methods in robotics and computer science have made large leaps in recent years toward demonstrating robotic capability for construction tasks (Petersen et al. 2019). However, while technically impressive, many of these studies have prioritized enhancing robotic capability and optimizing engineering outcomes, rather than directly testing biological hypotheses. As such, much previous work in this area has been more akin to bio-inspired design, which represents a one-directional flow of ideas.

Many early robotics approaches utilized centralized control and global state information (Augugliaro et al. 2014; Hsu et al. 2016), or limited global state information (Worcester et al. 2013; Yun et al. 2011) to enable robotic agents to work together. While demonstrating effective cooperative construction, these approaches do not reflect coordination in social insects, which cannot be governed by global state information or centralized control. Several studies have also explored decentralized control and construction involving stigmergic cues (Prasath et al. 2022; Soleymani et al. 2015; Stewart and Russell 2006; Theraulaz and Bonabeau 1995), or an "extended stigmergy" (Grushin and Reggia 2006; Werfel and Nagpal 2006). These investigations use approaches more similar to real social insect societies, as state information can be stored in the shared environment. Other work has explored "clustering" phenomena, in which robots guided by simple cues create localized piles of material with guidance primarily through environmental signals (Beckers et al. 2000; Deneubourg et al. 1991; Song et al. 2012). Such scenarios more closely mimic how biological collectives build nests; however, these approaches remain limited.

Prior studies have demonstrated success in coordinating construction with uniform building blocks (Fig. 6B) (Werfel et al. 2014), and some robotic systems have been capable of building or manipulating materials and structures autonomously (Petersen et al. 2019). However, for most organisms, the construction material used will be natural substrates with more complex contact laws, such as the cohesive soils in fire ant nests (Aleksiev et al. 2007; Monaenkova et al. 2015) or wax used by bees (Blomquist et al. 1980). Initial robotics work has used simplified versions of natural materials in the lab, including staples and artificially cohesive grains (Gravish & Goldman 2016; Hwang et al. 2024) (Fig. 6C), as well as toothpicks and urethane casting foam (Napp et al. 2012). However, work with these types of amorphous materials remains limited; thus, many robotics studies do not yet accurately reflect these complex mechanics.

Robophysics: using robots as tools for biology

While many studies in robotics have shown that biological systems can inform new technological advancements, recent work in "robophysics" (Aguilar et al. 2016) demonstrates that the inverse is also possible: simple robotic systems can be used to discover principles in biological systems (Aguilar et al. 2016). For example, a recent investigation fit robots with humidity sensors and programmed them to drip water during construction. This study was successfully able to replicate termite mound construction (Carey et al. 2021). This result supported the hypothesis that humidity can be used as a key environmental cue in termite nest construction. Another study used robots to test hypotheses concerning the mechanisms of cooperative transport in the ant *Novomessor cockerelli* (Wilson et al. 2018). By programming teams of robots to utilize different transportation strategies, the research team demonstrated that matching the speed of the slowest robot better recapitulated real ant behavior, and supported a mechanism by which ants might determine how to speed shift.

Robophysical modeling has also explored how environmental conditions such as crowding can affect collective outcomes in social insects. Robophysical models may be particularly advantageous in this regime, because they inherently capture the role of confinement within structures (Linevich et al. 2016), a common constraint in real social insect nests. For example, experiments on simple teams of robots transporting material through a confined tunnel revealed that a variety of tactics used by social insects can help prevent clogging, including unequal workload

Fig. 6 Robotic systems used to model construction behaviors of insect societies. **A** Robophysical models struggle to excavate model soil in confined conditions. Photocredit: Jeffrey Aguilar, Daria Monaenkova, Vadim Linevich, Will Savoie. **B** Demonstrations of autonomous robotic construction with building blocks. Photocredit: Eliza Grinnell (Werfel et al. 2014). **C** Robots used for construction with entangled granular materials. Photocredit: Daniel Soto, Joonha Hwang (Hwang et al. 2024). **D** Thousand-robot swam. Photocredit: Rubenstein et al. (2014)

distributions and spontaneous direction reversals (Aguilar et al. 2018) (Fig. 6A). Similarly, studies have demonstrated that allowing robots to modify their excavation probabilities based on collision rates leads to similar workload distributions to those seen in biological collectives (Aina et al. 2022). Finally, robophysical studies have been useful in understanding the role of the nest environment in modifying collective behaviors. A novel investigation constructed a robotic nest to investigate how bees respond to changes in their nest environments (Barmak et al. 2023), and demonstrated that temperature is an important cue for collective behavior within the nest.

Future directions and challenges

We believe robophysical models have high potential to inform our understanding of the material subtleties of construction and behavior in confined spaces. Nevertheless, significant technical and philosophical challenges remain before such studies will be common. First, until recently, fabrication technologies have had significant size and speed constraints, limiting most currently existing experimental robotic collectives to a few agents. Fortunately, recent years have seen a rise in rapid prototyping equipment and microelectronics kits. For instance, one study demonstrated swarm self-assembly by ~ 1000 simple robots into two dimensional shapes by utilizing local interactions and decentralized control (Rubenstein et al. 2014) (Fig. 6D).

An additional challenge in making robophysical models relevant to social insects will be in accurately capturing the role of nest material properties in construction. The interaction mechanics involved in nest construction, such as manipulation and grasping of cohesive grains (Aleksiev et al. 2007; Monaenkova et al. 2015), are surprisingly complex and not

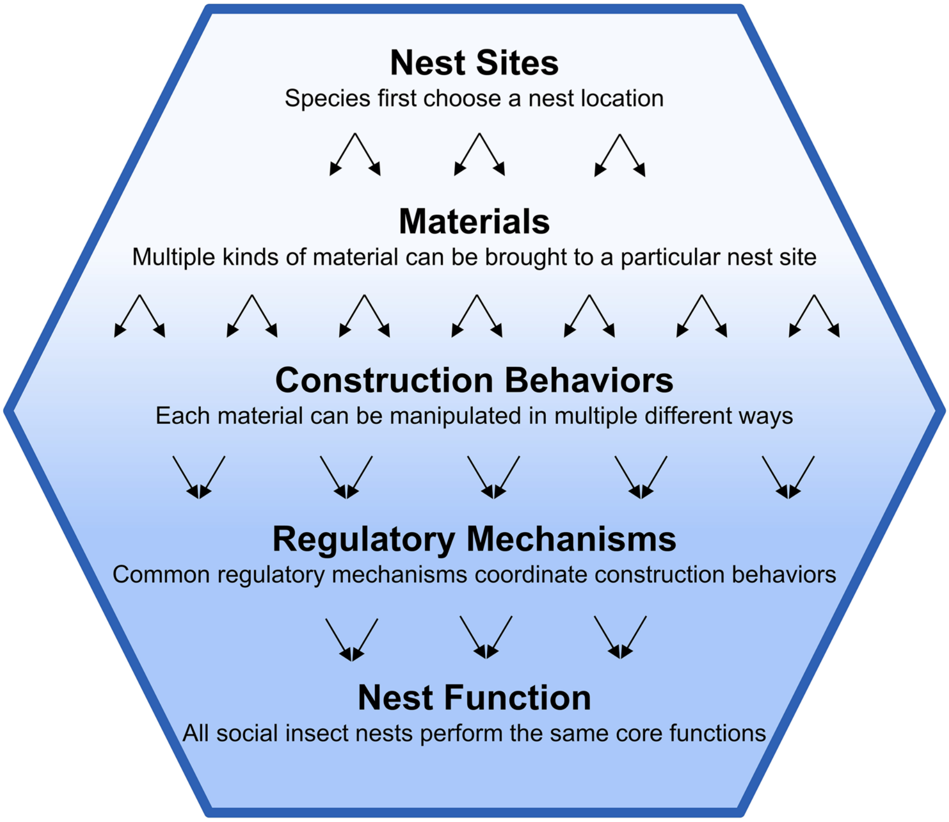


Fig. 7 Graphical representation of how diversity in nest characteristics compounds with each choice made by a social insect colony. Social insects first decide on a nest site. The colony can then decide on various materials to use for nest construction. Subsequently, there are many construction behaviors that individuals can use to build nests. Ultimately, however, this diversity in materials and building actions narrows back through a limited number of regulatory mechanisms for organizing behaviors ultimately leading to conserved nest functional optimum. Arrows represent increasing or decreasing number of decisions and gradient represents transition from the physical to the functional basis of nests

well-understood. Future studies should seek to better understand strategies employed by agents that directly manipulate, tear, or form cohesive substrates. Of course, no model ever fully captures the nuance of the system it replicates. As such, robophysical models may never recapitulate every aspect of the complicated interaction mechanics of an ant manipulating soil. However, we believe that these models will still test our understanding of social insect construction enough to provide new insights into how societies manipulate complex materials. In the future, robophysical approaches employing real nest substrates, or materials which mimic substrate properties, should be combined with direct observation and analysis of social insect material manipulation in an iterative process, wherein observation informs the robophysical modeling, which can in turn inform the questions asked by observers.

Finally, most robotic technologies today largely remain in the hands of engineers and computer scientists, and little crosstalk occurs between researchers in these fields and biologists. The disparate cultures between engineering and biology—including different funding sources, publications, methodologies, and questions prioritized—pose a challenge to interdisciplinary research. For example, biologists are often unfamiliar with the engineering and design principles necessary to design and operate a functional robot, while engineers are often unfamiliar with animal husbandry, and are not used to dealing with the high natural variability and noise in a biological system. We hope that increased publication of cross-disciplinary work in traditional pure biology and pure engineering journals will expose scientists in both fields to the techniques of the other, encouraging them to seek out collaborations across disciplines. These interdisciplinary conversations are essential to ensure that robotics studies are not simply “bio-inspired,” but rather grounded in physical and biological principles and seek to understand key phenomena.

Conclusion

Social insects construct a variety of remarkable nests, encompassing tiny, intricate dwellings in an acorn as well as vast underground labyrinths and giant, above-ground structures. From the first decision of where a nest is constructed through to its eventual modifications and repairs, every aspect of nest construction has consequences for a social insect colony. Different species manage these choices in different ways. Some species are generalists, while others have highly specific nest site requirements. Material selection is another crucial decision, and the materials used by insect societies vary widely. Construction behaviors range from excavation, favored by ants and termites, to manipulation of biologically modified foraged materials, favored by bees and wasps. Built structures are further modified by a plethora of unique variations on digging and shaping.

However, hidden amongst this extraordinary diversity are common challenges. All collectives must find a suitable place to live. Societies must be capable of modifying the environment to better suit their needs. In addition, individuals must coordinate into coherent collective construction. Collectives must deal with crowding and maintain the right internal environmental conditions to thrive. They must protect themselves from both predation and the elements.

We find that solutions to these common challenges repeatedly arise. Many species feature a sophisticated means of decision-making to coordinate nest site selection. Most species utilize some form of cohesive and moldable media to fashion optimized nest architecture. Mechanisms of coordinating construction behaviors are remarkably consistent across taxa. Stigmergy, positive and negative feedback loops, nestmate encounters, and genetic influences all emerge as common ways to regulate the activities of many builders. In addition, across taxa, the nest itself is a key recurring means of protecting residents and organizing colony-level collective behaviors.

We have also demonstrated how the diverse responses social insects have to these challenges directly result in further diversity of nest structure and function; every material difference has consequences, which compound at each stage from nest site selection through to the eventual results of nest architecture on collective behavior (Fig. 7). Interestingly, however, similarities still crop up at these later stages, even between species that have increasingly diverged in materials and behavior, suggesting that either certain convergent solutions are optimal, or that this diversity in nest construction leads somehow to conserved redundancies in nest function (Fig. 7).

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Declarations

Conflict of interest The authors declare no competing or financial interests.

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