Topology in motion: Geometry-driven defect dynamics in social wasp nests

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Emergent geometric order characterizes social insect nests, exemplified by paper wasps, which collectively build arrays of hexagonal cells to optimize space and mechanical stability. These arrays contain topological defects in the form of nonhexagonal cells, which disrupt the order of the nest. A disclination like a single pentagon or heptagon modifies angular geometry and introduces curvature, whereas adjacent pentagon-heptagon pairs form dislocations that retain planarity by offsetting angular mismatch at the cost of translational order. Unlike the malleable wax of honeybee combs, the rigid materials like plant fibers used by wasps limit structural remodeling, making such defect management more challenging. Here, we show the migration of dislocations through a sequence of discrete steps involving splitting into different types of disclinations. Defects propagate via local rearrangements of walls and vertices, analogous to star-triangle transformations and node release events that conserve topological charge, as confirmed by Burgers circuits. The shift was likely intended to promote hexagonal cell formation, with a secondary aim of driving the defect to the boundary. This was not achieved because subsequent nest growth displaced the boundary farther away from the defect region. Our results suggest that wasps achieve global architectural coherence through local geometric transformations that preserve topology, enabling decentralized construction under material constraints.

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I. INTRODUCTION

Biological assemblies, ranging from viral capsids, epithelial tissues to bird flocks, fish schools, and insect nests, display remarkable order [1–4], often emerging from simple, local interactions among many agents [5–8]. However, when such collective order is realized on a large scale, geometric constraints of tiling imposed by space-filling become unavoidable. This makes biological lattices a natural setting where the interplay of geometry and topology shapes structures.

Social insects such as paper wasps build nests comprising of hexagonal cells, and these structures harbor topological defects under geometric constraints, analogous to those observed in crystalline lattices such as graphene [3,9–11]. Although honeybees can reshape wax cells to correct or exploit such nonhexagonal cells [12–14], the hardened plant fiber walls of wasp nests constrain repair, making it more challenging to deal with them particularly after construction. These topological defects in honeycomb lattices can take the form of disclinations, like isolated nonhexagonal cells that introduce angular deficits or excesses, dislocations such as pentagon-heptagon (7-5) pairs, or higher order defects like Stone-Wales defects [3].

A single pentagon or heptagon embedded in a hexagonal lattice, such as the nest, disturbs the local orientational order and introduces intrinsic curvature [15]. This geometric frustration may be relieved either by deforming the lattice into the third dimension, or, alternatively by remaining planar at the cost of in-plane elastic distortion, whereby hexagonal cells become stretched or skewed away from their ordered pattern [16]. Moreover, the positive curvature generated by pentagonal topological defects plays a key role in the formation of icosahedral viral capsids [17]. However, when a five-sided and a seven-sided cell are placed adjacent to each other, their opposite angular distortions cancel, preserving the overall planarity of the lattice. This 7-5 pair forms a defect dipole or dislocation, which, unlike disclinations, preserves orientational order while distorting translational order because of an additional half row of hexagons extending from the defect to the boundary [3]. In our previous work, we established the baseline framework for understanding social wasp nests through the lens of condensed-matter physics. We analyzed nest structures as physical lattices and showed that, although they retain orientational order, they lack long-range translational order, rendering them closer to a hexatic state than to a perfect crystal. Accordingly, in the present paper we use the term topological defects (hereafter, defects) without any negative connotation, treating them instead as necessary and generically expected features of ordered systems.

While topological defects and their dynamics have been extensively studied in a wide range of ordered systems, including cosmological contexts [18], their occurrence and dynamics in biological architectures remain largely unexplored. Here, we report the emergence of a distinct topological defect state, a 7-4-7 triplet, observed during dislocation motion in a naturally occurring nest. This defect appears as an intermediate configuration that facilitates the shift of a dislocation within the nest through purely geometric rearrangements. The geometry-driven dynamics of such a defect state have not been previously documented in insect-built architectures. In Sec. II, we describe the details of the geometry-driven

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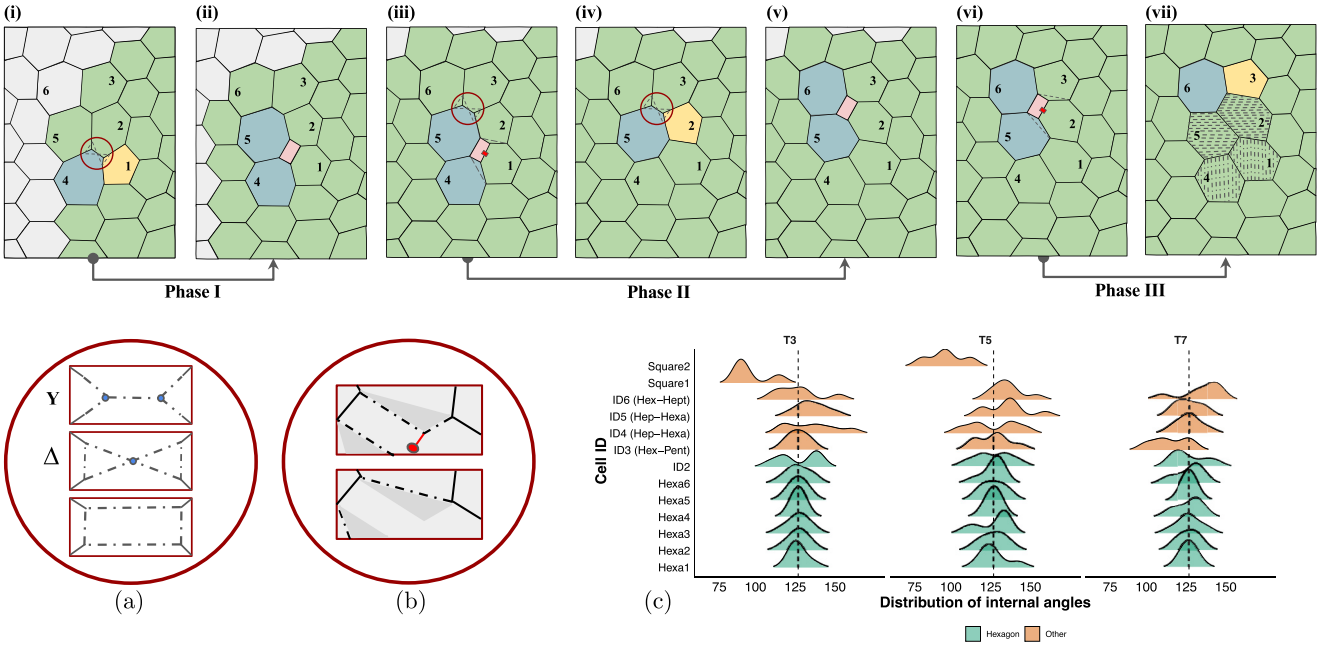

FIG. 1. A schematic representation of topological defects, their positions, and changes over time. (i) Phase I: Topological defect region being constructed (pentagon-heptagon pair at the nest margin) at a 40-celled stage. (ii) Phase I: Emergence of the 7-4-7 dislocation. [(iii), (iv), (v)] Phase II: Migration of 7-4-7 complex across the nest. Box (iv) illustrates the possibility of transformation to a 7-5 pair in Phase II. [(vi), (vii)] Phase III: Transformation of the 7-4-7 to a stable 7-5 defect state. Shaded cells mark cells that were previously nonhexagons, indicating the path of the defect motion. Panels (a) and (b) Expanded view of the circular regions indicating the Y-Δ transformations-node release, release-and-straighten events resulting in the quadrilateral. (c) Ridge line plot: The density distribution of internal cell angles of hexagonal (green, Hexa1-6 and ID2) vs nonhexagonal (orange) are plotted across time points (T3, T5, and T7 represent Phases I, II, and III, respectively) of migration. Quadrilaterals are shown as Square1 and Square2; ID4 and ID5 were cells that were heptagons transformed to hexagons; ID6 was a hexagon that was converted to a heptagon and ID3 was a hexagon that was converted to a pentagon.

dynamics defects within the nest and is different from the dislocation glides observed in the hexagonal structure of graphene [11] (summarized in Sec. IV). Section III characterizes the associated Burgers vector and the topological charges surrounding these defects. Finally, Sec. IV concludes by noting the implications of the observed topological defects for nests. Appendix A is a short note on the star-triangle transformation discussed in Sec. II A. Appendix B shows a time sequence of the nest growth. Appendix C is a representation of the time spent by wasps on the nest.

II. THE NEST CONSTRUCTION AND TOPOLOGICAL DEFECTS

The study was conducted on *Polistes wattii* species during the onset of their summer nesting. *P. wattii* is a primitively eusocial species with a widespread distribution (Asia and Middle East). They construct open, exposed paper combs that lack an outer envelope. Similar to other *Polistes* wasps, the nest is suspended from a narrow pedicel, or occasionally multiple pedicels, which anchor it to the substrate [19]. Nest construction in other *Polistes* species has been studied since Deleurance [20], who described it as an organized sequence of building behaviors. Later work showed that construction is driven not by fixed sequences or target geometry, but by local interactions between the builder and the existing structure, including body posture, local cell configuration, and structural constraints [21].

The nests themselves may be attached to the pedicel at various oblique angles. They are known to have two nesting cycles, one in the spring (March to May) and another in the summer (June to October) [22]. In our previous analysis of completed *Polistes wattii* nests in Ref. [3], 35 nests were inspected for topological defects in the form of nonhexagonal cells. In addition to this, growth-monitoring observations from six further nests were compiled. Across the combined dataset of 41 nests, nine contained at least one nonhexagonal cell. All nests were in the wild without any human interference. The detailed time-sequence analysis presented here is based on a single focal nest, whose growth trajectory revealed the construction of a topological defect. The wasp nest was imaged three times daily from a distance of 15 m (08:00–11:30; 13:30–16:00; 16:00–18:30; with the exception of poor visibility days). This nest expanded from 40 to 258 cells during the period of observation. We divided nest construction into three phases: initiation, migration, and stabilization, to illustrate the construction and rearrangement processes of the nonhexagonal complex. To analyze local rearrangements, the nest was treated as a planar network, with walls as edges and vertices as nodes (figures in Appendix B show an overview of the hexagonal net).

A. Phase I: Initiation

In the initial phase, when the nest comprised of 35 cells, we noted a pentagon-heptagon pair at the nest margin [Fig. 1(i)].

This pentagon (marked as 1) was transformed into a hexagon, facilitated by the emergence of a quadrilateral (via the addition and removal of vertices). Integration of this quadrilateral to the nest through its peripheral growth resulted in a second heptagon, thus forming a 7-4-7 cell complex [Fig. 1(ii)]. The emergence of this quadrilateral is an interesting phenomenon. The vertex supporting three edges has a Y-shaped configuration, and we predict that a Y-Δ transformation converts this into a triangular loop of three edges with three vertices in a Δ-shape. The Y-Δ mechanism (Appendix A) was first described in electrical network theory (the star-triangle transformation) and has been widely used for understanding planar lattice models in statistical mechanics [23].

With a pentagon as a defect, such a transformation enables the addition of a vertex to transform the pentagon into a hexagon (marked as 1, Fig. 1(iii)). Concurrently, an adjacent vertex undergoes a Y-Δ transformation to create two converging triangles with a shared vertex. Typically, since only vertices with three points are preferred by wasps, the four-point vertex is eliminated to form two edges whose straightening leads to the formation of a quadrilateral. The process locally accumulates material, observed as thickened walls in some of the cells after completion. The transformed hexagon (cell-1) was later observed to have a brood cap (see Appendix B).

B. Phase II: Migration

During this phase, the nest grows from 55 cells to a 125-cell stage. Phase II marks the stage where the spatial migration of the 7-4-7 defect within the nest has been identified. Changes in the internal wall angles of the nonhexagonal cell complex indicate a transient state, serving as a precursor to a translational shift. The distribution of interior angles for cells that remained hexagonal (mean ± sd = 120 ± 6.3 degrees) differed from cells that experienced transformations (e.g., ID4, ID5 in Fig. 1(c); range of mean angles = 90°–129°). Migration was found to occur incrementally, one cell at a time, with the annihilation and subsequent reconstruction of another quadrilateral hinging on a pivot cell [marked as 5 in Fig. 1(c)]. This pivot cell retained its defect state through the process. The annihilation of the quadrilateral on one face of the pivot cell occurred via a release-and-straighten, which involves an edge cut opposite to the pivot cell ('release'), followed by straightening of the adjacent edges ('geometric relaxation'). Its subsequent construction on a different face was possibly a repetition of the Y-Δ transformations-node release events as during Phase I. The removal or addition of the quadrilateral also transformed a neighboring heptagon into a hexagon (cell-4), and vice versa (cell-6), completing the one-unit displacement of the entire 7-4-7 defect. If the quadrilateral was not rebuilt, a pentagon-heptagon (7-5) pair could have emerged at this stage (indicated in Fig. 1(iv)), signaling a change in defect type rather than its position. The observed construction of a second quadrilateral, ensuring cell-2 stays hexagonal (brood caps visible in Appendix B), hinted towards a choice made at this stage to continue the translational mobility upwards (in the direction of the nest growth) as an attempt towards 'ironing' out nonhexagonal cells.

C. Phase III: Stabilization

In Phase III, a similar sequence of transformations as seen in Phase II was observed without the last step of reconstruction. Readjustments to internal wall angles stretch the quadrilateral before being annihilated. Removal of a vertex from the adjacent cell (marked as 3, Fig. 1(vii)) converts it to a pentagon, while the pivot cell (marked as 6, Fig. 1(vii)) retains its heptagonal form. A resultant 7-5 pair is formed two cells away from the Phase I pentagon location. This state remains consistent for the rest of the nest's growth trajectory. Figure 2 provides a detailed sequential overview of nest growth, depicting the progressive changes in the positions of the defect complex across growth phases.

The persistence of the 7-5 cell pair, despite repeated local angle readjustments, indicates that defect motion reaches a locally accommodated endpoint without global reorganization, motivating the arguments below on the limits and possibilities of emergence of defect complexes in such nests. Local changes alone cannot repair a topological defect without inducing global change to a system, the latter not being an easy possibility in dried paper nests. The defects initially nucleated near the boundary, from where they could, in principle, have been expelled out of the system. However, as collective nest construction proceeded and the boundary shifted outward, such expulsion became increasingly ineffective and operationally costly. Instead, the colony grew around the defect dipole, thereby extending the associated dislocation line, an extra row of hexagons terminating at the dipole, which was incorporated into the growing structure and persisted as a stable topological feature [3]. Additionally, given the relatively small size of the quadrilateral, no functional advantage for brood care or storage is evident (in honeybee nests quadrilaterals were used as filler cells [12]), and therefore we predict that their appearances are incidental and may not be adaptive. The three phases demonstrate an apparent local motion of the topological defect, exhibiting transformations in form and spatial position only in the short range. This informs our proposition that the alternating *Y-Δ transformations-node release* and *release-and-straighten* events can propagate the defect's movement, at the expense of removal of walls and the construction of new walls. From an evolutionary perspective, defects indicate that wasps allow variation in their architectural structures. This flexibility appears to result from modular construction rules that rely on coordinated, simple algorithms. These algorithms may facilitate variation in the spatial organization of cells, which emerge from decisions made by individuals when multiple possible configurations are available at each step [16,24,25].

III. TOPOLOGICAL INVARIANTS: BURGERS VECTORS AND CHARGES

To evaluate whether the magnitude of distortion provides cues for this displacement, we computed the Burgers vector, which represents the *net lattice translation* around a closed circuit enclosing the dislocation (the circuit was drawn manually by tracing an equal number of cell centers in each direction; in a defect-free region, the loop closes with zero excess). The Burgers vector associated with the dislocation

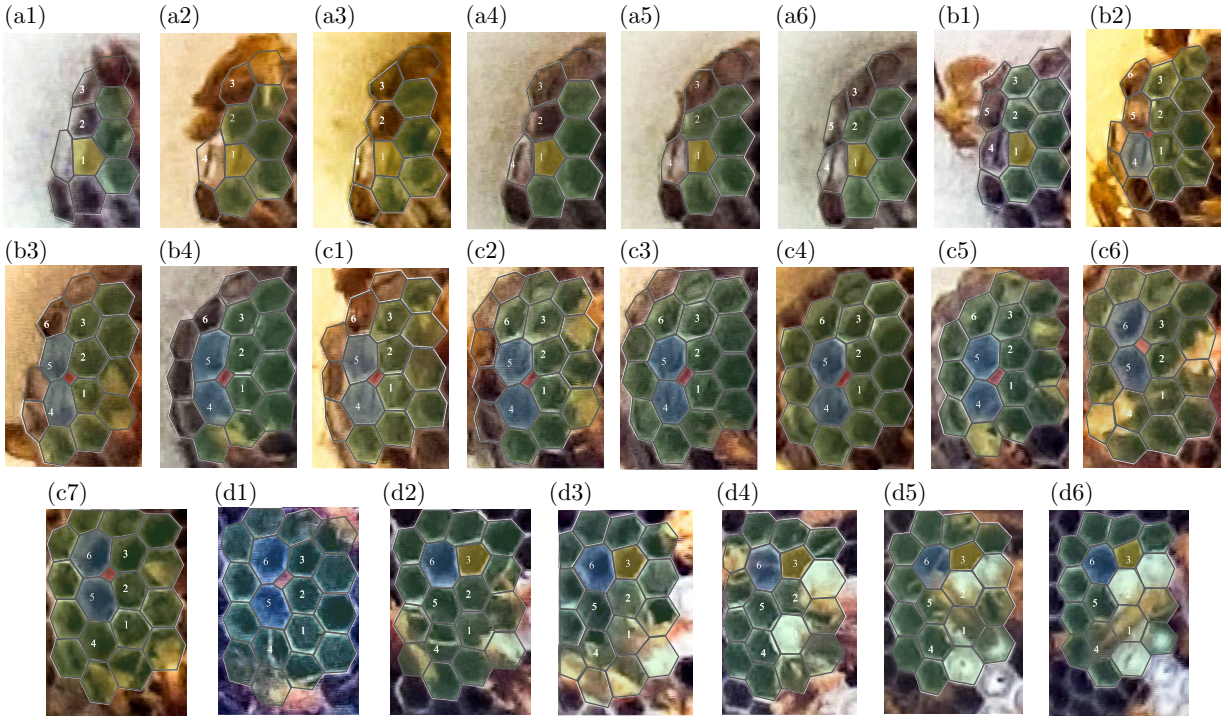

FIG. 2. (a1)–(a6) Topological defect region being initialized (pentagon and heptagon at the periphery of a 40-celled stage) in early Phase I. (b1)–(b4) Emergence of quadrilateral as defect enters lattice, forming a 7-4-7 complex in Phase I. (c1)–(c4) Visible changes in internal angles of cells along with growth in the nest in Phase II. (c5)–(c7) Migration of 7-4-7 complex in Phase II. (d1)–(d2) Transformation of 7-4-7 to 7-5 defect after migration, in Phase III. (d3)–(d6) Stabilized 7-5 pair in Phase III. Eggs (brood caps) appear as white-filled cells in subpanels (d3)–(d6). Hexagons are outlined in green; nonhexagons are outlined as follows: quadrilateral (red), heptagons (blue), pentagons (yellow), overlaid on the corresponding nest images.

was comparable in both Phase II (7-4-7) and Phase III (7-5) configurations (Fig. 3). Thus, the construction of a relatively complex defect state does not appear to confer the advantage of reduced distortion. This invariance arises from the topological character of the defects, specifically the relationship between dislocations and pairs of disclinations (known as a disclination-dipole). The dipole direction, defined as the vector from the center of the seven-sided cell to the center of the five-sided cell, determines the orientation of the dislocation. The associated Burgers vector lies in-plane and is perpendicular to this dipole. In more complex configurations, such as the 7-4-7 defect, the structure contains two dipoles, each formed by a 7-4 pair. The vector sum of these dipoles (of zero total charge) results in a net dipole aligned with that of the original 7-5 pair. Consequently, the transformation 7-5↔ 7-4-7 preserves the Burgers vector, and maintains the global topological character of the nest (Fig. 3).

Interestingly, the transformations done by wasps also reflect topological charge conservation. A hexagonal lattice (wasp nest) with sixfold rotational symmetry allows for five types of topological defects (disclinations): three-, four-, five-, seven-, and eight-sided polygons, all of which have three-point vertices. A defect carries a topological charge q such that a cell with fewer than six sides (such as five, four, or three) carries a positive charge, while a cell with more than six sides (seven, eight, nine, etc.) carries a negative charge (an overview of charges is given in Table I). A closed loop around a disclination does not produce any Burgers vector; instead, it

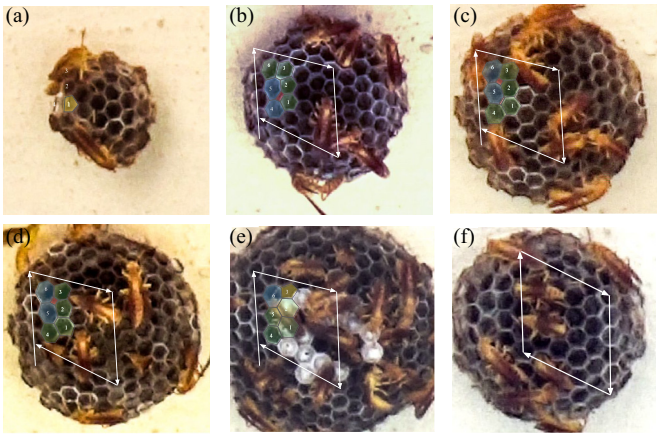

FIG. 3. Burgers circuit at various stages of nest growth depicting the vector with additional displacement in the defect region, in contrast to the region without defect where the loop closes without an excess. (a) Initial pentagon visible during Phase I. (b) The Burgers vector drawn around the 7-4-7 complex before migration, indicating the extra step. (c) The vector around the 7-4-7 region during migration via annihilation of a quadrilateral and emergence of another. The Burgers vector (d) for the 7-4-7 complex postmigration, one unit cell away from the beginning of Phase II; (e) for the stabilized 7-5 defect during Phase III, located two unit cells away from initialization in Phase I; (f) of the hexagonal lattice without defects (enclosing hexagonal cells).

TABLE I. Topological charge $q = (6 - n)$ assigned to polygonal cells in a three-coordinated hexagonal lattice, where n is the number of sides. Topological charge is also known as winding number [27,28]. It reflects the degree of distortion from ideal hexagonal order and influences the geometric orientations of the surrounding hexagonal cells.

Polygon type	n	Topological charge
Quadrilateral	4	$(6-4) = +2$
Pentagon	5	$(6-5) = +1$
Hexagon	6	$(6-6) = 0$ (no defect)
Heptagon	7	$(6-7) = -1$

produces a change in the orientation of the starting hexagon by an angle given by $q\frac{\pi}{3}$. For example, $+1 = (+2) + (-1)$, a pentagon $(+1)$ is topologically equivalent to a quadrilateral $(+2)$ combined with a heptagon (-1); this implies that 7-5 has the same net topological charge as a 7-4-7. Furthermore, the purported Y-Δ transformations and the resulting quadrilateral may help transition from a pentagon to an ideal hexagon. However, while respecting local topological charge conservation, these attempts to 'iron out' defects merely relocate charges as zero net charge cannot be achieved by local moves.

Properties of construction material and geometric constraints appear to drive emergence, movement, and annihilation dynamics in wasp nests. Such dynamics were also seen in liquid crystals [26]. These dynamics suggest a behavioral signature: If defects are being 'ironed out' via local Y–Δ transformations (Fig. 4 in Appendix A), activity of most individuals should concentrate at the defect and briefly perturb growth symmetry; to test this, we mapped wasp occupancy across the nest and calculated diameter ratios (Figs. 5 and 6). Since wasps may remain on cells for brood care, larval feeding, inspection, or other social interactions, and local occupancy can also be influenced by brood developmental stage, the occupancy data in Fig. 6 in Appendix C are to be interpreted only as indicative of time spent for building behavior. In Phase I, new cells accumulated along defect-free margins, producing an elliptical outline. The diameter ratios deviated from 1 (range of DR = 0.87 to 1.16), indicating that defect construction transiently disrupted nest symmetry. While perfect nests with isotropic growth and radial symmetry are rarely found in nature, the variations result from underlying building rules [16,25,29]. During Phases II–III, a wasp frequently occupied the defect site, consistent with pulp deposition, inspections, and vertex-wall readjustments. Time spent at the defect region was slightly higher than the nondefect regions (mean: 66.6 s vs 41.6 s, Fig. 6). Given the short observation windows and ambiguity of occupancy, this pattern is not direct evidence of repair or pulp deposition, but is consistent with localized activity near the defect during shape adjustment.

IV. DISCUSSION AND SUMMARY

The mechanisms and consequences driving the observed geometric rearrangements are not isolated from those guiding nest construction. Nest construction has been explained largely through template-based and stigmergy-based mechanisms [2,30,31]. Stigmergy refers to a class of indirect interactions mediated by modifications of a shared environment, often through persistent traces or structures. Such environmental cues can enable collective organization without direct pairwise coupling. In other words, stigmergy involves agents modifying the environment in ways that influence subsequent actions, whereas template-based activity relies on a fixed or externally imposed environmental patterns [32]. In nest construction, coordination and regulation largely arise from local information provided by the developing nest structure, together with multiple stochastic decisions by individuals [29]. Based on prioritized selection pressures, the functional significance of the physical properties of the nest may contribute to building behavior [33].

In social wasps, nest building is generally understood through a stigmergic framework, in which individuals respond to local cues provided by the partially built structure rather than to a global plan [34,35]. In *Polistes*, potential building sites are not equivalent: New-cell initiation is influenced by local structural constraints, especially the number of existing/shared walls, with sites supported by multiple adjacent walls being more likely to be used than more exposed sites [36]. This perspective is important for interpreting the transitions observed in our nests. Central cells generally represent older, more developed regions of the comb, whereas peripheral cells often include newly initiated or actively expanding cells; consequently, central and peripheral regions may differ in wall height, cell completeness, and local support. We therefore interpret the observed growth patterns as the outcome of local construction rules operating within a spatially heterogeneous comb.

Topological defects with nonhexagonal cells and their occurrence as triplets and pairs have been observed in insect wings, *Xenopus* tail epithelia, and honeybee nests [12,37]. In our study, during Phase I and II, their continual wall-angle adjustments suggest that some of these defects are transient features. In graphene and single-walled nanotubes (SWNTs), the motion of a pentagon-heptagon dislocation on a hexagonal lattice proceeds via two well-established mechanisms: (i) glide, parallel to the Burgers vector, and (ii) climb, perpendicular to it [10,11]. Glide involves the transient formation of a Stone-Wales defect through the interaction of two 5-7 dislocation pairs, followed by annihilation of the original pair. In contrast, climb requires the creation of an octagon accompanied by a dangling bond, and is therefore energetically costly. Neither mechanism is followed in the wasp nests; instead, defect migration parallel to the Burgers vector occurs through a sequence of 7-4-7 disclinations, reflecting an alternative mode of dislocation dynamics. The results highlight a distinct path of defect management in which geometric and topological constraints, rather than reversible energetic relaxation, guide rearrangements during irreversible biological construction. Although our analysis draws on observations from a single focal nest (more than 25 wasps over the course of a month), these findings demonstrate that nonhexagonal cells can rearrange during natural nest growth, a conclusion about the possibility rather than prevalence, and thus provide a foundation for future studies aimed at quantifying how broadly this process operates.

Our analysis showed that a nonhexagonal cell near the pedicel was ultimately transformed into a hexagon (initially a pentagon in Phase I, was later transformed into a hexagon, which was observed to have the brood cap). Wasps are known to utilize parts of their own bodies as self-referential tools to measure wall lengths, which may enable them to distinguish between hexagonal and nonhexagonal cells. We hypothesize that in smaller nests (150 cells), eggs are preferentially laid in centrally located cells [38], and such rearrangements may serve to ensure that these core cells are hexagonal (overview of nest growth shown in Fig. 5). This may be shaped by functional constraints: Pentagons and heptagons cannot accommodate eggs as snugly as hexagons, and given the limited plasticity in egg size [39], nonhexagonal cells are likely avoided for oviposition. Thus, geometric corrections could be a colony-level strategy to maximize the proportion of usable central brood cells. Cells vary in size and shape depending on what they may contain, their developmental stage, and cues from neighboring cells. In *Polistes*, where castes are not discrete, a linear dominance hierarchy is thought to structure labor and space: Dominants (typically the queen) occupy the center, while workers and subordinates cluster peripherally with limited overlap [40,41], providing behavioral context for who undertakes such corrections.

From a physical perspective, a dislocation, characterized by a nonzero Burgers vector, introduces a topological mismatch in the lattice, equivalent to the insertion of a half row of hexagons from the defect to the boundary. In a defect-free nest, identical local growth rules followed by the wasps ensure global compatibility of the hexagonal architecture [29–31] The introduction of a pentagon-heptagon pair, however, breaks this compatibility; although the local construction rules remain unchanged, they become globally inconsistent due to the lattice misalignment imposed by the defect. As a result, the mismatch must be accommodated at larger scales. Biologically, this implies that wasps not directly involved in defect motion can continue to obey invariant local rules, but the colony as a whole must adjust to the global consequences, such as the creation of additional cells. Put simply, our findings reveal that the emergent coordination of many individuals enables the topological reorganization of ordered biological structure.

DATA AVAILABILITY

Images used in the analysis are provided in the Appendix. Image sequences from multiple time points have also been deposited in Figshare [42]. The extracted data and code are available from the corresponding author upon request.

APPENDIX A: STAR-TRIANGLE (Y-Δ) TRANSFORMATION

The star-triangle or Y-Δ transformation is a graph operation that replaces a three-edge star, i.e., a central vertex connected to three terminal vertices, with a triangle among those terminals, and vice versa. This is shown in Fig. 4. For electrical circuits, the transformation preserves the effective resistance while in statistical mechanics the partition function is preserved. In general, the transformation helps in reducing or expanding a graph while keeping its external connectivity intact.

APPENDIX B: PROGRESSIVE GROWTH OF THE WHOLE NEST

In this Appendix, we show the nest at different sampled time points, highlighting the collective effort of many wasps in the growth process. In Fig. 5, the background is the ceiling from which the nest is hanging by a pedicel. Throughout the growth process, the nest remains approximately planar and parallel to the ceiling. The growth increments shown here correspond to changes observed between successive sampling time points.

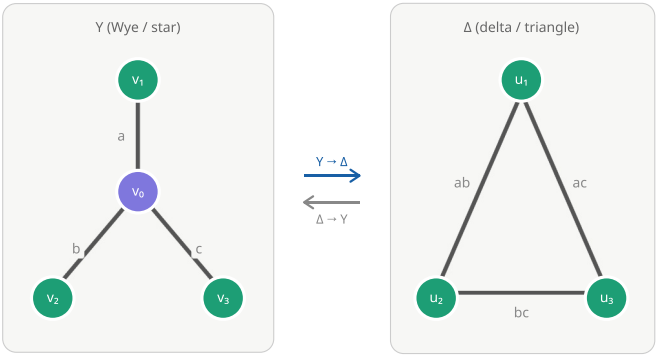

FIG. 4. Y-delta transformation depiction: The Y–Δ transformation is a mathematical tool used to simplify complex networks. In a Y-shaped junction, three vertices (v_1, v_2, v_3) are connected to a central point (v_0) by the edges a, b, c. This arrangement can be replaced by an equivalent triangular, or Δ-shaped, connection among the same three outer points (u_1, u_2, u_3) with edges ab, bc, ac. It is a way of simplifying a local branching pattern while keeping the overall connections between neighboring regions unchanged. The transformation does not mean that the structure itself changes from a Y shape into a triangle. Instead, it provides an equivalent network representation that preserves the connections among the surrounding points. This approach is useful for analyzing complex biological architectures because it reduces the complexity of local branching arrangements while retaining the effective connectivity of the network.

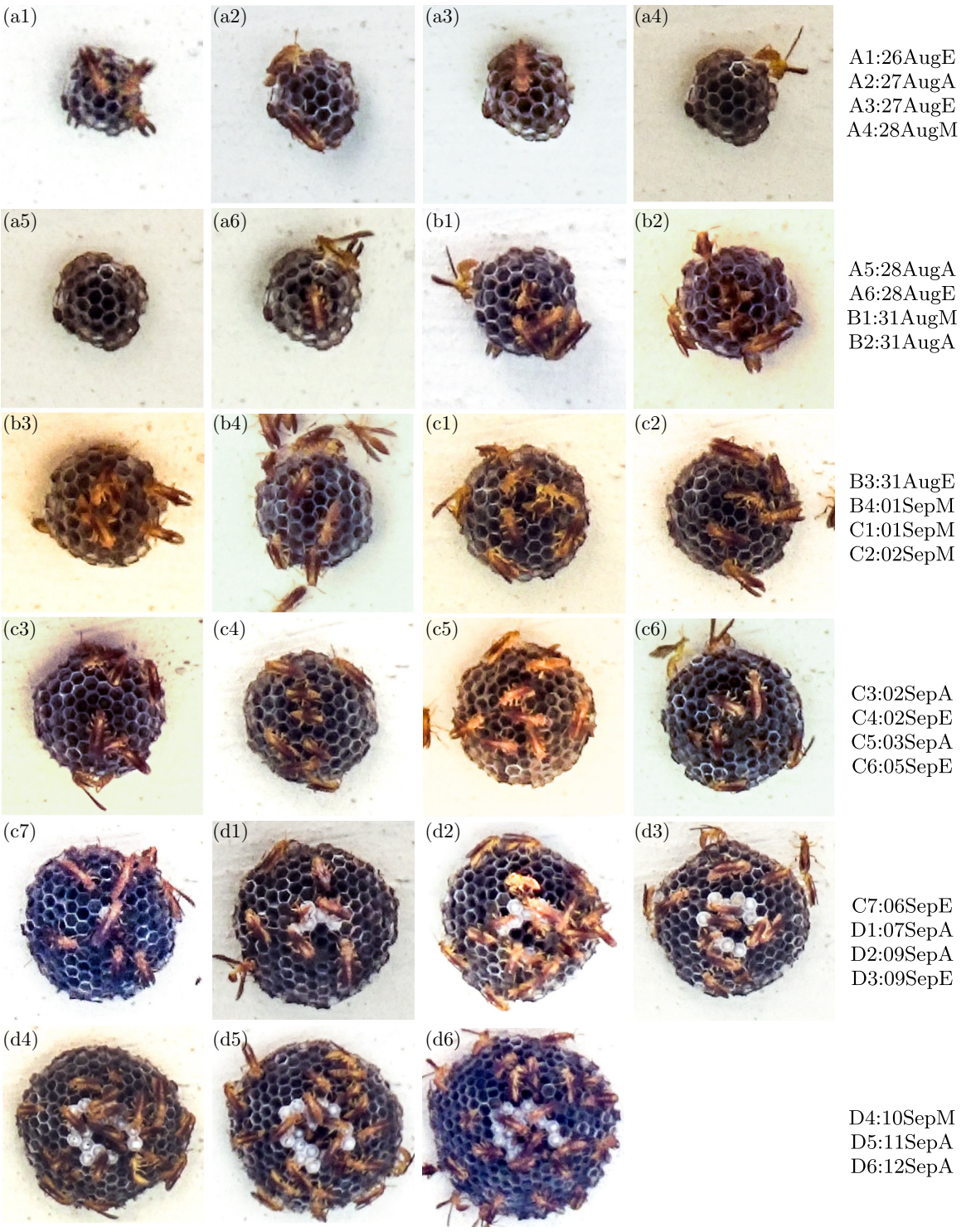

FIG. 5. Sequential images documenting progressive growth of the paper wasp nest (sampling period shown alongside each panel). Eggs (brood caps) appear as white-filled cells. Note the rectangular cell in panel (b4) (left half) near the boundary [see also (c4)], which subsequently evolves into a 7–5 disclination pair (a dislocation) by panel (c7). This pair persists through later stages and remains visible up to panel (d6). The legends on the right indicate the timestamps. The abbreviations are Aug: August; Sep: September; M: Morning; A: Afternoon; E: Evening. Sampling periods were defined as M: 8:00–11:00 am, A: 13:30–16:00, and E: 16:00–18:30.

APPENDIX C: TIME SPENT BY WASPS ON THE NEST

From recordings spanning the growth phases, we analyzed snapshots of 30-s intervals in which a wasp occupied each cell (Fig. 6). Over the growth phases, the number of wasps observed within the frame of recording varied between 4 and 26.

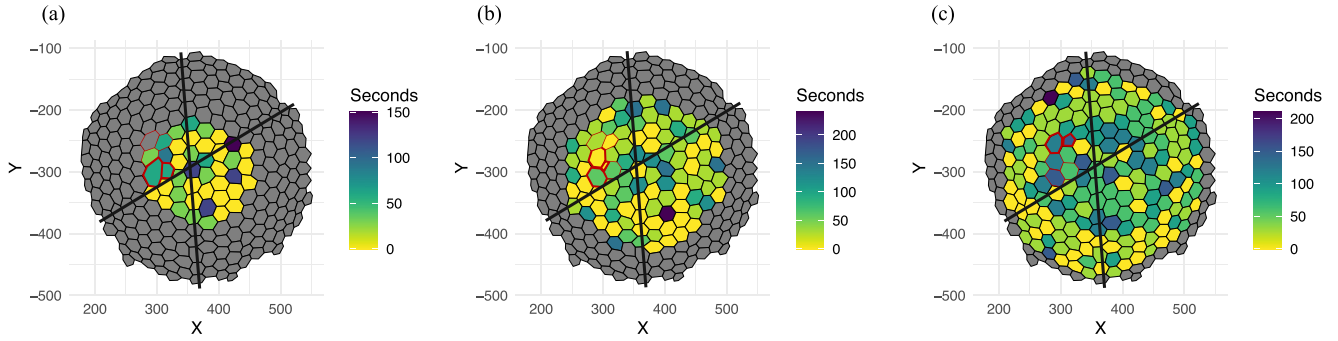

FIG. 6. Time spent by wasps on the nest depicted as heatmaps. Gray cells indicate the overall size of the nest towards the end of its growth period. Darker filled colors in the cells indicates longer time spent by wasps in a cell. For each phase, 8–10 min of sampled snapshots were aggregated to estimate occupancy. (a) Phase I: occupancy pattern with the initial 7–5 defect (red outline) in the upper left quadrant. (b) Phase II (premigration): occupancy around the 7–4–7 complex (red outline) as it shifts further within the upper left quadrant. (c) Phase III (poststabilization): final occupancy pattern with the stabilized 7–5 defect (red outline farther into the upper left quadrant).

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