

Active screws: Emergent active chiral nematics of spinning self-propelled rods

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Several types of active agents self-propel by spinning around their propulsion axis, thus behaving as active screws. Examples include cytoskeletal filaments in gliding assays, magnetically driven colloidal helices, and microorganisms such as the bacterium *Myxococcus xanthus*. Here, we develop a model for spinning self-propelled rods on a substrate, and we coarse grain it to derive the corresponding hydrodynamic equations. If the rods propel purely along their axis, they form an active nematic at high density and activity. However, spinning rods can also roll sideways as they move. We find that this transverse motion turns the system into a chiral active nematic. Thus, we identify a mechanism whereby individual chirality can give rise to collective local chiral flows. Finally, we analyze experiments on *M. xanthus* colonies to show that they exhibit chiral flows around topological defects, with a chiral activity about an order of magnitude weaker than the achiral one. Our work reveals the collective behavior of active screws, which is relevant to colonies of social bacteria and groups of unicellular parasites.

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I. INTRODUCTION

Across scales, Nature has taken advantage of the principle of a screw to drive motion. At the molecular scale, in so-called gliding assays, both microtubules and actin filaments are propelled and spun by carpets of molecular motors [1]. At the cellular scale, rod-shaped bacteria like *Myxococcus xanthus* and *Flavobacterium johnsoniae* glide on surfaces by spinning around their body axis [2–10]. Other bacteria like *Treponema primitia* swim by spinning their helical bodies [2]. At larger scales, starfish embryos [11] and algae like *Chlamydomonas reinhardtii* [12] and *Volvox* [13] also swim while spinning. Beyond the living world, screwlike propulsion was achieved in synthetic helical micropropellers driven by magnetic fields [14–16] or chemical reactions [16,17], and it was also found in simulations of active droplets [18,19]. All these systems share a key feature: Self-propulsion and spinning share the same axis, and the self-propulsion speed is proportional to the spinning rate. These systems therefore behave as active screws.

In contrast, most work on active chiral particles has focused on objects on a plane that spin around the axis perpendicular to the plane [20–23] [Figs. 1(a) and 1(b)]. Systems with this type of chiral motion include bacterial and sperm cells close to surfaces [24–28], microtubules [29], FtsZ filaments [30], as well as L-shaped self-propelled colloids [31] and magnetic spinners [32,33]. Another class of spinning active particles is rollers, such as Quincke rollers [34], which spin around an axis in the same plane but perpendicular to the self-propulsion axis [Fig. 1(c)]. In all these cases, the axes of rotation and translation are different. Here, we introduce *active screws* as a class of active particles for which the axes of rotation and translation are the same [Fig. 1(d)].

Rotation and translation along the same axis are common in microswimmers, for example, in bacteria propelled by helical flagella. In that case, however, the swimmer is torque-free, and hence the rotation of the flagella is compensated by a counterrotation of the cell body [2,35,36]. The swimmer therefore experiences no net rotation, and it exerts a torque dipole. In contrast, we focus on active screws moving on surfaces, such as gliding bacteria, which rotate their entire body in the same direction and are therefore driven by a torque monopole. Recent work started to describe the intracellular flows that power this type of gliding motility [37,38] and to analyze single-cell trajectories [39–41]. However, the collective behavior of active screws is only beginning to be addressed [42–44].

Here, we develop a microscopic model of active screws and we coarse grain it to obtain the continuum equations that capture their collective behavior. Our results show that, if

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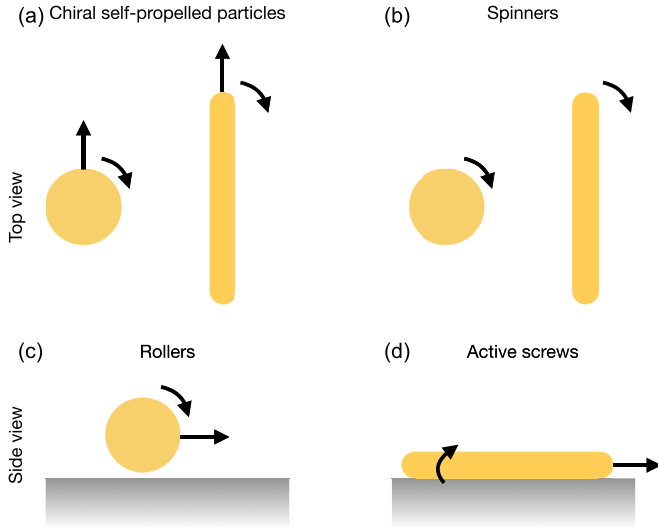


FIG. 1. Classes of active chiral particles. (a) Chiral self-propelled particles propelling on the plane and spinning around the axis perpendicular to it. (b) Spinners do not translate. (c) Rollers spin around an in-plane axis perpendicular to their self-propulsion. (d) Active screws spin and self-propel along the same axis.

active screws propel purely along their axis, they form an active nematic. The theory of active nematics was recently used to explain cell flows and the formation of cell layers in colonies of *M. xanthus* [45,46]. However, the connection between the continuum equations and the microscopic dynamics of this gliding bacterium was not established. Our results provide this connection: We give the coefficients of the continuum theory in terms of the microscopic parameters. Finally, we generalize our findings to active screws that also roll sideways, thus adding a transverse component of motion. In this case, we obtain the equations of chiral active nematics. We thus identify a mechanism whereby the chirality of individual constituents can give rise to collective chiral effects. Overall, our work generalizes the theory of self-propelled rods [47,48] to spinning particles, and it can be tested in colonies of gliding bacteria.

II. MICROSCOPIC MODEL OF ACTIVE SCREWS

We propose a model of active screws as point particles with an intrinsic axis corresponding to the orientation of the rod that they represent. We model the spinning of active screws via their spinning rate $\dot{\phi}_i$ as [Fig. 2(a)]

$$\dot{\phi}_i = \omega \Phi_i(t) + \frac{\tau_i}{\xi_s}. \quad (1)$$

The first term accounts for self-spinning at a rate ω . Moreover, gliding bacteria experience stochastic spinning reversals [49]. We include them via a dichotomous noise $\Phi_i(t)$ that switches between $+1$ and -1 with Poisson statistics, such that $\langle \Phi_i(t) \Phi_j(t') \rangle = \delta_{ij} \exp(-2f_{\text{rev}}|t - t'|)$, where f_{rev} is the average reversal frequency. Similar to a recent model for eukaryotic cell doublets [50], the second term accounts for spin torque transfer between neighboring screws [blue in Fig. 2(c)], $\tau_i = \sum_{j \neq i} \tau_{ji}$, which affects the spinning rate through the spin friction coefficient ξ_s . We assume a torque

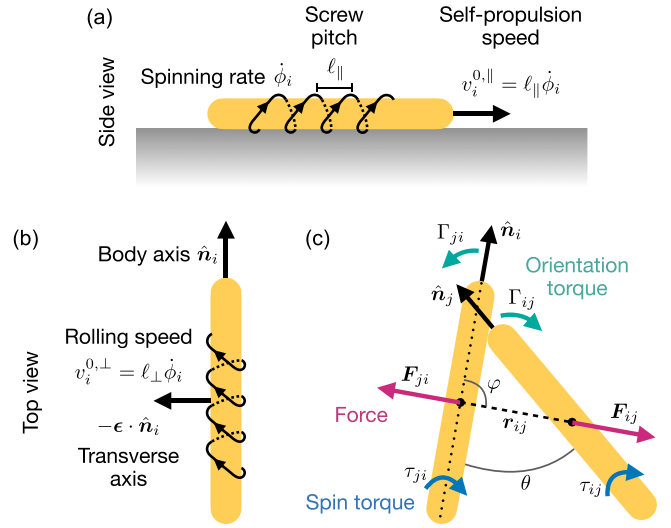


FIG. 2. Motion and interactions of active screws. (a) An active screw spinning at a rate $\dot{\phi}_i$ with a pitch $\ell_{\parallel}$ propels along its axis at a speed $v_i^{0,\parallel} = \ell_{\parallel} \dot{\phi}_i$. (b) An active screw can also propel sideways by rolling at a speed $v_i^{0,\perp} = \ell_{\perp} \dot{\phi}_i$. (c) The interactions between active screws include forces, torques that change their orientations, and torques that change their spinning rate.

transfer proportional to the relative velocity between the rod surfaces, and hence to the sum of their spinning rates: $\tau_{ij} = \tau_r(r)(\dot{\phi}_i + \dot{\phi}_j) \cos \theta$, where $r = |\mathbf{r}_{ij}|$ is the distance and $\cos \theta = \hat{\mathbf{n}}_i \cdot \hat{\mathbf{n}}_j$ is the projection between the two rods [Fig. 2(c)]. By affecting the spinning rate, this torque can make neighboring particles either speed up or slow down depending on whether they spin in the opposite or the same direction, respectively.

We then describe screw motion by coupling the spinning rate to translation, such that the self-propulsion speed of rod i along its axis is $v_i^{0,\parallel} = \ell_{\parallel} \dot{\phi}_i$. Here, $\ell_{\parallel}$ is the pitch of the screw, i.e., the distance it advances in one revolution [Fig. 2(a)]. This relation assumes that the screws transduce all the spinning into propulsion, without slipping. This assumption is consistent with measurements on gliding bacteria, where the transduction of spinning into propulsion relies on cell-substrate binding provided by proteins called adhesins [2,3,5–7]. We also allow the rods to roll sideways as a result of their spinning, moving at a speed $v_i^{0,\perp} = \ell_{\perp} \dot{\phi}_i$ perpendicularly to the rod axis $\hat{\mathbf{n}}_i \equiv (\cos \theta_i, \sin \theta_i)$, where $\ell_{\perp}$ is the rolling pitch [Fig. 2(b)]. If rolling occurs without slipping, then $\ell_{\perp} = 2\pi R$, with R the rod radius. Thus, the rod positions $\mathbf{r}_i$ follow

$$\frac{d\mathbf{r}_i}{dt} = \ell_{\parallel} \dot{\phi}_i \hat{\mathbf{n}}_i - \ell_{\perp} \dot{\phi}_i \boldsymbol{\epsilon} \cdot \hat{\mathbf{n}}_i + \frac{\mathbf{F}_i}{\xi_t}, \quad (2)$$

where $\boldsymbol{\epsilon}$ is the Levi-Civita symbol and $\mathbf{F}_i = \sum_{j \neq i} \mathbf{F}_{ji}$ is the force of interaction with neighboring rods, which changes rod positions through the translational friction coefficient ξ_t . We assume the force between two rods to be central and proportional to their projection: $\mathbf{F}_{ij} = F_r(r) \cos \theta \hat{\mathbf{r}}_{ij}$ [purple in Fig. 2(c)]. Brownian motion is typically negligible in gliding cells since they are well attached to the substrate. Therefore, we ignore translational noise.

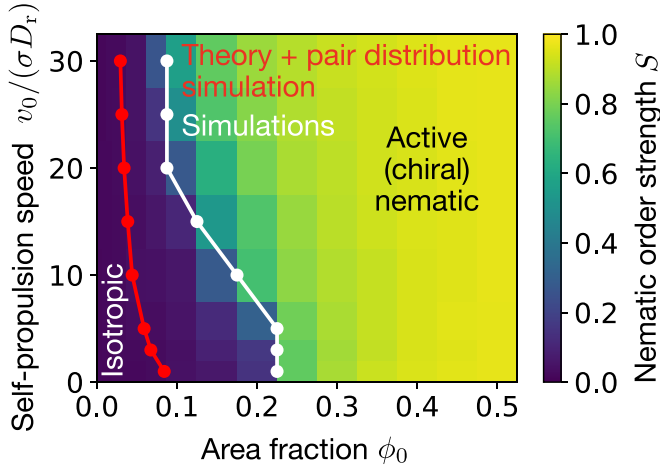


FIG. 3. Activity-induced nematic order. Phase diagram displaying the nematic order strength S (see Appendix B). In the simulations, the self-propulsion speed is given by $v_0 = \ell_{\parallel} \omega$. Following Ref. [55], the numerical phase boundary (white) is identified from the points of steepest ascent of the measured S . The theoretical phase boundary (red) is predicted by setting $a_Q = 0$ in Eq. (5). The nematic phase is chiral in the presence of rolling.

Finally, the orientation angle of the rods evolves as

$$\frac{d\theta_i}{dt} = \frac{\Gamma_i}{\xi_r} + \eta_i(t), \quad (3)$$

where $\Gamma_i = \sum_{j \neq i} \Gamma_{ji}$ is the orientation torque from interactions with other rods [green in Fig. 2(c)], which affects the orientation angle through the rotational friction coefficient ξ_r , and $\eta_i(t)$ is a Gaussian noise with strength given by the rotational diffusivity D_r : $\langle \eta_i(t) \eta_j(t') \rangle = 2D_r \delta(t - t') \delta_{ij}$. We assume nematic orientational interactions: $\Gamma_{ij} = \Gamma_r(r) \sin(2\theta)$ [Fig. 2(c)]. Unlike for other classes of active chiral particles [Figs. 1(a) and 1(b)], here we introduce no self-rotation in the orientation angle θ_i .

III. EMERGENCE OF NEMATIC ORDER

To study the emergent phases of active screws, we perform simulations of the Langevin equations of our model (Appendixes A and B). For simplicity, we ignore the projection of the repulsive interaction forces. We find that the system transitions from an isotropic to a nematic phase by increasing either the global area fraction of particles ϕ_0 or the self-propulsion speed v_0 (Fig. 3). Therefore, an increase in activity can induce the emergence of nematic order.

This result is consistent with previous works on self-propelled rods, which found that activity decreases the threshold for the isotropic-nematic transition [47,51,52]. This result, however, contrasts with most models of active nematics, for which nematic order is incorporated directly in the free energy as it is assumed to arise from the passive alignment interactions between the constituents [47]. Moreover, our system is dry, meaning that friction completely screens hydrodynamic interactions. Thus, the possibility for activity-induced nematic order in our system is different from a recently predicted instability whereby isotropic wet active

nematics can order due to a feedback between active flows and nematic order [53].

To predict the isotropic-nematic transition, we coarse grain the microscopic Langevin equations (1)–(3). First, we eliminate Eq. (1) by introducing it into Eq. (2). The stochastic reversals encoded in $\Phi_i(t)$ give rise to an effective rotational diffusivity $D_r^{\text{eff}} = D_r + 2f_{\text{rev}}$ on timescales $t \gg f_{\text{rev}}^{-1}$ [54]. Second, for this reduced set of Langevin equations, we write the corresponding Smoluchowski equation and we break it into the Bogoliubov-Born-Green-Kirkwood-Yvon (BBGKY) hierarchy to obtain an equation for the one-particle distribution function (Appendix C). From it, we obtain the following equation for the nematic order-parameter tensor:

$$\partial_t \mathbf{Q} = a_Q[\rho] \mathbf{Q} \quad (4)$$

to lowest order in gradients (Appendix D). Here,

$$a_Q[\rho] = \frac{\gamma_2}{\pi \xi_r} \rho - 4D_r \quad (5)$$

is the growth rate of the nematic order. If $a < 0$, the isotropic state with $\mathbf{Q} = \mathbf{0}$ is stable. If $a > 0$, it is unstable to the appearance of nematic order. Thus, the condition $a_Q[\rho] = 0$ determines the phase boundary for the isotropic-nematic transition. The coefficient γ_2 in Eq. (5) is given by

$$\gamma_2 = \int_0^{r_T} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \Gamma_0 \sin^2(2\theta) g(r, \varphi, \theta) \quad (6)$$

in terms of the torque amplitude Γ_0 (Appendix A) and of the pair correlation function $g(r, \varphi, \theta)$ between two particles separated by a distance vector $\mathbf{r}$ given by the polar coordinates (r, φ) and with a relative orientation θ . We measure this function in simulations (see Appendix B and Fig. 9) to calculate γ_2 and thus predict the phase boundary for the isotropic-nematic transition (Fig. 3, red), which captures the trend of the numerical results. Note that the isotropic phase, including its correlations, captured by $g(r, \varphi, \theta)$, and its stability, determined by $a_Q[\rho]$, are not affected by rolling, which has consequences only in the nematic phase.

Moreover, turning off reversals in simulations by setting $f_{\text{rev}} = 0$ slightly shifts the onset of nematic order (Fig. 5), and it gives rise to polar flocks (Fig. 6), which produce stronger and longer-lived polarity fluctuations (Fig. 7), consistent with experiments [46]. At high densities, oppositely oriented flocks can jam and phase separate (Figs. 6 and 8).

Finally, the nematic phase is locally chiral in the presence of rolling, as we show below. Yet, Eq. (4) lacks the term $\sim \Omega \epsilon_{\alpha\gamma} Q_{\gamma\beta}$ describing the global self-rotation of the axis of nematic order introduced in previous works on chiral active nematics [56,57] and observed in microtubule carpets [43]. Therefore, systems of active screws do not break chiral symmetry globally, but only locally. This difference is because, in contrast to previous models of chiral active rods [Fig. 1(a)], active screws spin around the orientation axis [Fig. 1(d)], which therefore does not self-rotate.

IV. ACTIVE CHIRAL NEMATIC PHASE

Turning to the active chiral nematic phase, we obtain its hydrodynamic equations from our coarse-graining procedure

(Appendix E). For the rod density field, we obtain

$$\partial_t \rho = -\nabla \cdot \mathbf{J}; \quad \mathbf{J} = v_{\parallel}[\rho] \mathbf{p} - v_{\perp} \boldsymbol{\epsilon} \cdot \mathbf{p} - \zeta_1 \rho \nabla \rho. \quad (7)$$

The first term in the flux $\mathbf{J}$ is advection along the polarity field $\mathbf{p}(\mathbf{r}, t)$ at a local speed $v_{\parallel}[\rho] = \omega \ell_{\parallel} - \zeta_0 \rho$. This speed is produced by the screw motion at a self-spinning rate ω , and it decreases with the density field $\rho(\mathbf{r}, t)$. The coefficient ζ_0 , given in Eq. (E1), captures the slowdown resulting from repulsive interactions between rods, which is responsible for motility-induced phase separation [58,59]. Torque transfer between neighboring screws, captured by the τ_i term in Eq. (1), speeds up slower particles and slows down faster ones, such that it has no net effect at the coarse-grained level. The second term in Eq. (7) corresponds to a flux perpendicular to the polarity at a speed $v_{\perp} = \omega \ell_{\perp}$ driven by rolling motion. The transverse speed $v_{\perp}$ does not have a slowdown effect because we assume that the system is statistically achiral, and hence the repulsive forces from the right and the left of a reference rod cancel out. Finally, the last term in Eq. (7), with ζ_1 given in Eq. (E4), is a diffusive flux induced by repulsive interactions between rods [60].

The polarity field follows the following equation:

$$\begin{aligned} \partial_t \mathbf{p} = & -\nabla \cdot (v_{\parallel}[\rho] \mathbf{Q}) - \frac{1}{2} \nabla (v_{\parallel}[\rho] \rho) + \nabla \cdot (v_{\perp} \boldsymbol{\epsilon} \cdot \mathbf{Q}) \\ & + \frac{1}{2} \boldsymbol{\epsilon} \cdot \nabla (v_{\perp} \rho) + \nabla \cdot (\zeta_1 \mathbf{p} \nabla \rho) - D_r^{\text{eff}} \mathbf{p}. \end{aligned} \quad (8)$$

The first and second terms are polarity contributions emerging from the divergence of the nematic order-parameter tensor $\mathbf{Q}$ and from density gradients. Due to self-propulsion, this polarity then produces density currents in Eq. (7), which are a key ingredient of dry active nematics [47,61]. In the presence of rolling, with $v_{\perp} \neq 0$, the polarity gets additional transverse contributions represented by the third and fourth terms in Eq. (8). Finally, the last term captures the decay of the polarity field due to orientational noise with strength D_r^{eff} . This decay is faster than that of the nematic order in Eq. (4) due to the contribution of reversal events, which affect the polarity but not the nematic order. Thus, even though both types of order can exist [62], reversals favor the emergence of nematic in front of polar order.

The density current relates to the velocity field $\mathbf{v}(\mathbf{r}, t)$ as $\mathbf{J} = \rho \mathbf{v}$. For a system with uniform density $\rho = \rho_0$, using the steady-state solution of Eq. (8), we obtain a velocity field that corresponds to that produced by active stresses of a chiral nematic on a substrate [56,57,63–65]:

$$\mathbf{v} = \frac{1}{\xi} \nabla \cdot \boldsymbol{\sigma}_{\text{act}}; \quad \boldsymbol{\sigma}_{\text{act}} = -\zeta \mathbf{Q} + \zeta_c \boldsymbol{\epsilon} \cdot \mathbf{Q}. \quad (9)$$

Here, following the convention in the field, we take $\mathbf{Q}$ to be the dimensionless nematic order parameter, whereas $\mathbf{Q}$ in Eq. (8) is its density, with units of squared inverse length. In Eq. (9), ξ is the friction coefficient, and ζ and ζ_c are the coefficients for achiral and chiral active stresses, respectively. Our results relate these coefficients to the parameters of the active-screw model as

$$\frac{\zeta}{\xi} = \frac{v_{\parallel}^2[\rho_0] - v_{\perp}^2}{D_r^{\text{eff}}}, \quad \frac{\zeta_c}{\xi} = \frac{2v_{\parallel}[\rho_0] v_{\perp}}{D_r^{\text{eff}}}, \quad (10)$$

with $v_{\parallel}[\rho_0] = \omega \ell_{\parallel} - \zeta_0 \rho_0$ as discussed below [Eq. (7)]. This result completes our derivation and establishes the connec-

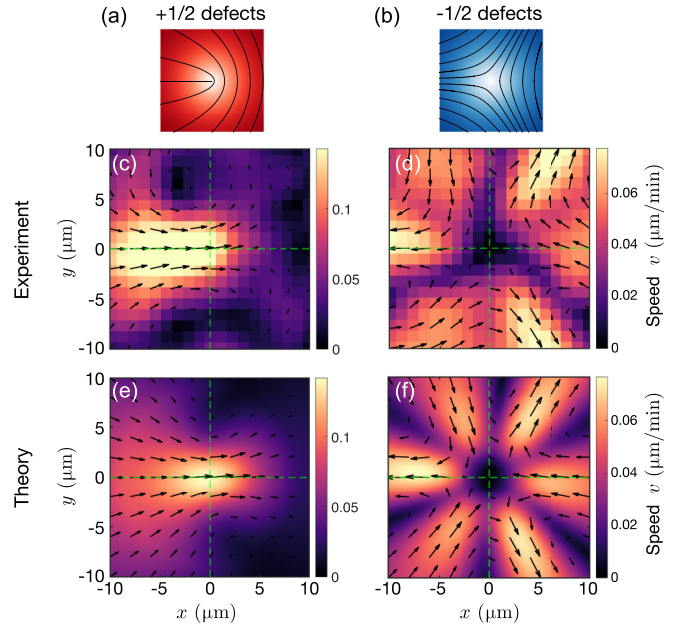


FIG. 4. Chiral flows around topological defects. (a) and (b) Defect schematics show the order parameter (color) and the director field (lines). (c) and (d) Experimental flow fields from Ref. [46]. (e) and (f) Fit of active chiral nematic theory (see Appendix F and Ref. [46]). Parameter estimates are listed in Table I.

tion between the microscopic parameters and hydrodynamic coefficients.

V. CHIRAL FLOWS AROUND TOPOLOGICAL DEFECTS

We now compare the predictions of our theory to recent measurements of flow fields around topological defects in colonies of the gliding, spinning bacterium *M. xanthus* [45,46] (Fig. 4). Fitting the continuum theory of active nematics to the experimental data gave values of $\zeta/\xi \approx 2 \mu\text{m}^2/\text{min}$ [45]. Here, ignoring rolling ($v_{\perp} = 0$), we use independent measurements of the self-propulsion speed [54,66], $v_{\parallel} = 1.3 \mu\text{m}/\text{min}$, and of the effective rotational diffusivity [54], $D_r^{\text{eff}} = 0.34 \text{ min}^{-1}$, to predict $\zeta/\xi \approx 5 \mu\text{m}^2/\text{min}$ from Eq. (10). This value, predicted from our microscopic model, is slightly larger but comparable with the fit results to experimental data.

Next, we consider the effects of rolling ($v_{\perp} \neq 0$), which give rise to chiral flows. Chiral flows around defects have

TABLE I. Parameter estimates for the bacterium *M. xanthus*. The last two estimates are obtained in this work (see text).

Symbol	Description	Estimate
S_0	Strength of nematic order	0.992 [45]
ℓ	Defect core size	$2.5 \mu\text{m}$ [45]
ζ/ξ	Active stress/friction	$2 \mu\text{m}^2/\text{min}$ [45]
ε	Friction anisotropy	0.7 [45]
D_r^{eff}	Effective rotational diffusivity	0.34 min^{-1} [54]
$v_{\parallel}$	Longitudinal self-propulsion speed	$1.3 \mu\text{m}/\text{min}$ [54,66]
ζ_c/ξ	Chiral/achiral active stress	0.17
$v_{\perp}$	Rolling speed	$0.04 \mu\text{m}/\text{min}$

been previously proposed to arise in fibrosarcoma cell layers [67,68]. Here, we analyzed the experimental data of Ref. [46] and we found that the flows have a nonzero chiral component. The chirality is visible in Figs. 4(c) and 4(d) as the slight upward flows observed along the $\hat{x}$ axis. Fitting the theory of incompressible chiral active nematics to the data (Fig. 4, see details in Appendix F), we found that $|\zeta_c|/\zeta \approx 0.11$ for $+1/2$ defects and $|\zeta_c|/\zeta \approx 0.24$ for $-1/2$ defects. From the results of the fits, using Eq. (10) and the value of D_r^{eff} listed above, we estimate a rolling speed $v_\perp \approx 0.02\text{--}0.06 \mu\text{m}/\text{min}$. All parameter estimates are listed in Table I.

Our analysis revealed chiral flows around topological defects in colonies of *M. xanthus*. While our theory does not attempt to achieve quantitative agreement with the experiments, it identifies a possible mechanism for the chiral flows: The rolling motion of bacteria due to their spinning-based gliding motility. Rolling was achieved in helical microswimmers [69] and is also performed by fruit fly larvae [70]. Although we know of no direct evidence for rolling in gliding bacteria, our results suggest that chiral cellular flows around defects might be an indirect evidence for this type of cellular motion. Our estimates indicate that the rolling speed could be more than an order of magnitude smaller than the longitudinal self-propulsion speed. Hence, rolling might have been overlooked in the experiments. Based on these findings, future experiments can both search for direct evidence of rolling and investigate alternative mechanisms for chiral flows, including the emergence of polar order during defect unbinding [71].

VI. DISCUSSION AND OUTLOOK

We introduced a microscopic model for active screws—a class of active chiral particles that spin around their axis of self-propulsion [Fig. 1(d)]. Compared to other classes of active particles, which are described by their position and orientation, active screws have an additional degree of freedom: their spinning rate. The spinning rate contributes to (1) the speed at which active screws propel themselves forward, (2) the speed at which they roll sideways, and (3) the spin torque transferred among neighboring screws. Whereas previously studied active chiral particles also spin, they do it perpendicularly to their axis of self-propulsion [Figs. 1(a)–1(c)]. Moreover, in most cases studied so far, the spinning rate was constant, independent of the self-propulsion speed and of interactions with other particles. Hence, the spinning rate was so far a parameter instead of a degree of freedom as in the case of active screws.

We predicted the collective behavior of active screws by coarse graining the microscopic model. We obtained continuum equations that correspond to a chiral active nematic, albeit with important features such as the absence of active rotation of the nematic axis due to the fact active screws spin around their own axis. Our derivation shows how the microscopic screw and rolling motion give rise to macroscopic achiral and chiral active nematic stresses, respectively. This micro-macro connection is directly relevant for colonies of gliding bacteria, where single-cell decisions are thought to control collective behaviors [54,72,73].

We then analyzed experimental data from Refs. [45,46] to reveal the presence of chiral flows in colonies of *M. xanthus*. We estimated the corresponding active chiral stresses to be an order of magnitude weaker than the achiral ones. Using the micro-macro connection, we estimated the values of microscopic parameters, such as the rolling speed, from experimental data. Our results could potentially also explain collective chiral flows observed in colonies of other bacteria with screwlike propulsion, such as *C. gingivalis* [74] and *F. johnsoniae* [75]. Overall, using our theory of active screws, we propose that a possible mechanism for emergent chiral flows is the transverse rolling motion that can take place when a screw spins against a substrate. We propose to test these ideas against possible alternative mechanisms in future experiments.

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APPENDIX A: SIMULATION DETAILS

Here, we describe the simulations of our microscopic model. We simulate the dynamics of $N = 2500$ active Brownian particles based on Eqs. (1)–(3). The particles move in a two-dimensional square box of side L with periodic boundary conditions. The particles interact via pairwise forces $\mathbf{F}_{ji}$, orientational torques Γ_{ji} , and spin torques τ_{ji} . To model excluded volume interactions, we take $\mathbf{F}_{ji}(\mathbf{r}_i - \mathbf{r}_j) = -\nabla_{\mathbf{r}_j} U(\mathbf{r}_i - \mathbf{r}_j)$, with U being the Weeks-Chandler-Andersen (WCA) potential,

$$U(\mathbf{r}) = \begin{cases} 4U_0 \left[\left(\frac{\sigma}{|\mathbf{r}|} \right)^{12} - \left(\frac{\sigma}{|\mathbf{r}|} \right)^6 \right], & \text{if } |\mathbf{r}| \leq r_{\text{WCA}}, \\ 0, & \text{if } |\mathbf{r}| \geq r_{\text{WCA}}, \end{cases} \quad (\text{A1})$$

where U_0 is the potential strength, σ is the particle diameter, and r_{WCA} is the force cutoff distance. For simplicity, in our simulations, we ignore the projection $\cos \theta$ of the force between rods that was introduced in Sec. II. To model the nematic alignment between rods, we take a short-range torque $\Gamma_{ji}(\mathbf{r}_i - \mathbf{r}_j, \theta_i - \theta_j)$ given by

$$\Gamma_{ji}(\mathbf{r}, \theta) = \begin{cases} \Gamma_0 \sin(2\theta), & \text{if } |\mathbf{r}| \leq r_\Gamma, \\ 0, & \text{if } |\mathbf{r}| \geq r_\Gamma, \end{cases} \quad (\text{A2})$$

where Γ_0 is the orientation torque strength and r_Γ is the torque cutoff distance, which we set to $r_\Gamma = 2\sigma$.

For the spin torques in our simulations, we use a modified version of the one presented in Sec. II to improve numerical stability: Consider two interacting active screws i and j of length L at relative angle $\theta = \theta_j - \theta_i$, spinning at rates $\dot{\phi}_i$ and $\dot{\phi}_j$. The overlap of the two particles is given by the projection $L|\cos \theta|$; this is the effective length over which the screws

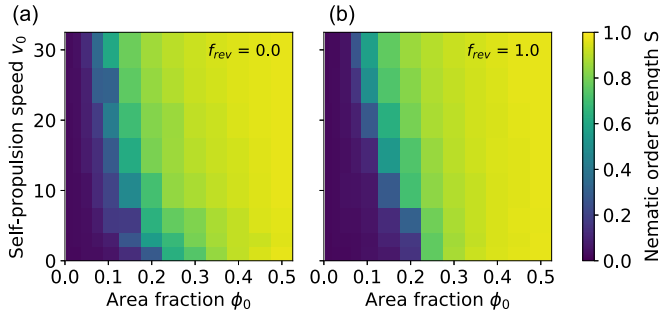


FIG. 5. Nematic order in simulations. Phase diagrams showing activity-induced nematic order both without reversals [panel (a)] and with reversals at a rate $f_{rev} = 1$ [panel (b)].

can exert spin torques on each another. Let us now consider the spin torque exerted by screw j on screw i , which we assume to be proportional to the effective overlap and the relative surface velocity, which is approximately $\dot{\phi}_i + \dot{\phi}_j \cos(\theta)$. Here, the cosine appears since flipping the orientation of j will flip its spinning axis. As a result, the spin torque reads

$$\tau_{ji}(\mathbf{r}, \theta, \dot{\phi}_i, \dot{\phi}_j) = \begin{cases} \tau_0 |\cos(\theta)| (\dot{\phi}_i + \dot{\phi}_j \cos(\theta)), & \text{if } |\mathbf{r}| \leq r_\tau, \\ 0, & \text{if } |\mathbf{r}| \geq r_\tau, \end{cases} \quad (\text{A3})$$

where τ_0 is the spin torque strength and the cutoff $r_\tau = 2\sigma$ the same as r_Γ .

We set simulation units by defining the particle diameter σ and the inverse rotational diffusivity D_r^{-1} to be the units of distance and time, respectively. The simulation is performed using an explicit Euler-Mayurama method for the time evolution, with time step $\Delta t = 10^{-5}$, for up to time $t_{\max} = 150$, and with parameter values $U_0/\xi_t = 2.5$, $\Gamma/\xi_r = 10$, $f_{rev} = 1$, $\tau_0 = -0.05$, $\xi_s = 1$, $\ell_{\parallel} = 6.64\pi$, and $\ell_{\perp} = 0.23\pi$. To build the phase diagram, we then vary the self-propulsion speed $v_0 = \ell_{\parallel}\omega$, which we vary by adjusting the spinning rate ω , and the global area fraction $\phi_0 = N\pi(\sigma/2)^2/L^2$, which we vary by adjusting the system size L .

APPENDIX B: SIMULATION RESULTS

After running the simulations to a steady state, we characterize the state of the system as follows. As either the self-propulsion speed v_0 and/or the area fraction ϕ_0 increases, nematic order emerges. We quantify it via the nematic order strength $S = (1/N) \langle |\sum_{j=1}^N e^{i2\theta_j(t)}| \rangle_t$, which we show in Figs. 3 and 5.

In the absence of direction reversals, we observe polar clusters [Fig. 6(a)]. To characterize the emergence of such local polar order, we obtain the polarity correlation length ℓ_p defined by $C_p(r) = \langle \mathbf{p}(\mathbf{r}) \cdot \mathbf{p}(\mathbf{0}) \rangle \sim e^{-r/\ell_p}$. We plot ξ_p in Fig. 7, which shows that reversals readily destroy local polar order by destabilizing polar clusters. Without reversals, at high area fractions, we find that the polar clusters collide often against one another and form aggregates [Fig. 6(b)], which leads to phase separation (Fig. 8). We quantify phase

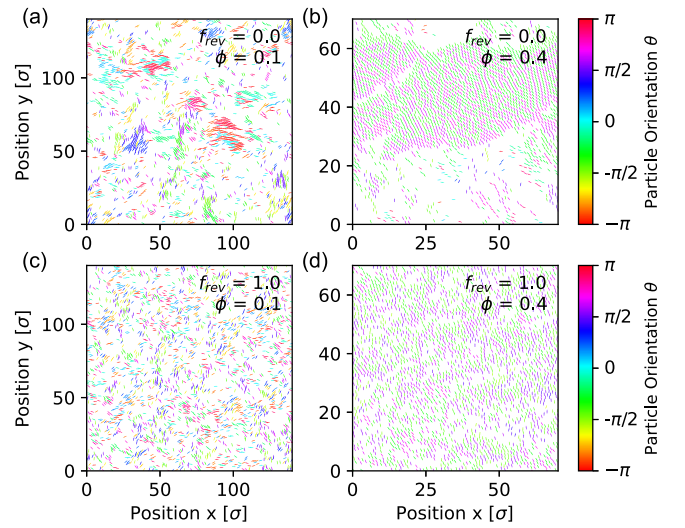


FIG. 6. Simulation snapshots of active screws with and without polarity reversals. Without reversals, active screws form polar clusters at low area fraction [panel (a)], whereas at high area fraction, they phase separate into a dilute and a dense nematic phase [panel (b)]. With reversals, there are no polar clusters at low area fraction [panel (c)]. Similarly, at high area fraction, there is no phase separation, but the system achieves a state with nematic order [panel (d)]. All four snapshots are taken at $v_0 = 10$ in simulation units (see text).

separation via the distribution of local area fractions, $P(\phi)$ [Fig. 8(a)]. At low area fraction ϕ_0 , the distribution has a single peak, reflecting density fluctuations of a single phase [Fig. 8(a), red]. However, at higher area fractions ϕ_0 , the distribution has two peaks, which correspond to the coexisting dense and dilute phases [Fig. 8(a), blue].

To predict the isotropic-nematic transition using the theory that we develop in Appendix D, we measure the pair distribution function $g(r, \varphi, \theta)$ from our simulations. The pair distribution is a function of the distance vector $\mathbf{r}$ connecting two particles—expressed here in polar coordinates as the distance r and the polar angle φ —and of the relative orientation θ of the two particles. We compute $g(r, \varphi, \theta)$ as outlined in Ref. [55]:

$$g(r, \varphi, \theta) = \frac{2\pi \mathcal{N}(r, \varphi, \theta)}{A(r) N t_{\text{run}} \rho \Delta \theta}, \quad (\text{B1})$$

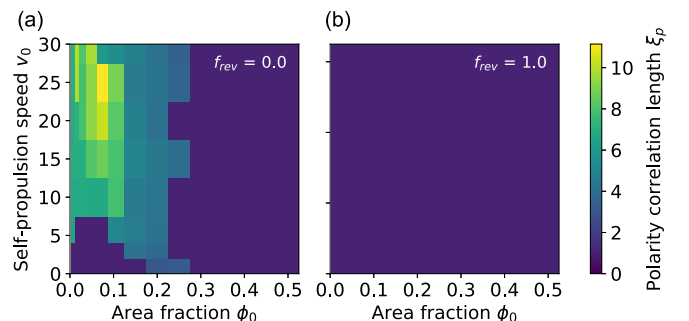


FIG. 7. Local polar order in simulations. Phase diagrams showing the polarity correlation length (see text) both without reversals [panel (a)] and with reversals at a rate $f_{rev} = 1$ [panel (b)].

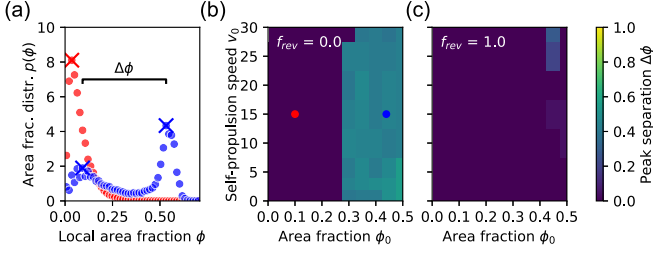


FIG. 8. Phase separation in simulations. (a) Probability distribution of local area fractions. A bimodal distribution, with two peaks (blue), indicates phase separation. Phase diagrams showing the separation in area fraction between the peaks in the area-fraction distribution shown in panel (a), both without reversals [panel (b)] and with reversals at a rate $f_{\text{rev}} = 1$ [panel (c)]. If the distribution has a single peak, the peak separation is set to zero.

where $\mathcal{N}(r, \varphi, \theta)$ is a histogram of the number of particles at the given distance, positional angle, and relative orientational angle, which we obtain numerically from our simulations. In the denominator, $A(r) = r\Delta r\Delta\varphi$ is the area of an annular segment of radial width Δr and angular opening $\Delta\varphi$ at distance r . Here, Δr , $\Delta\varphi$, and $\Delta\theta$ are the bin sizes for distance, positional angle, and relative orientational angle, respectively. Finally, N is the particle number, ρ the number density of particles, and t_{run} the number of snapshots that are used to generate the histogram. To obtain the phase boundary in Fig. 3, we chose bins of size $\Delta r = 0.5$ and $\Delta\varphi = \Delta\theta = \pi/180$, and we

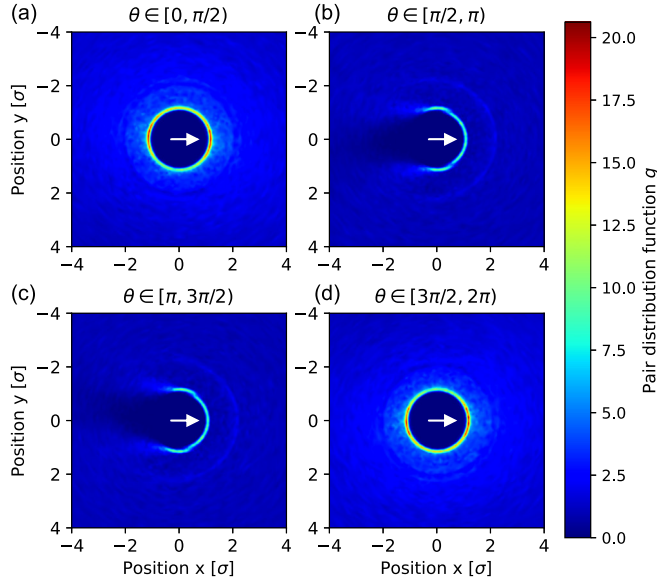


FIG. 9. Pair distribution function sampled from simulations. Pair distribution function $g(r, \varphi, \theta)$ sampled numerically using Eq. (B1), which we use to compute the nematic order growth rate in Eqs. (5) and (6). Here, we show g for $\phi = 0.05$, $v_0 = 10$, and $f_{\text{rev}} = 0$, in the isotropic phase. The panels correspond to each of the four quadrants of the relative orientation θ between two particles, as indicated above the plots. The white arrows indicate the orientation of the reference particle. The pair distribution functions for $f_{\text{rev}} \neq 0$ (not shown here) are qualitatively similar to the ones shown here.

averaged over $t_{\text{run}} = 100$ snapshots in simulations with $N = 2500$ particles. We show an example of the pair distribution function in Fig. 9.

APPENDIX C: COARSE GRAINING: FROM THE MICROSCOPIC MODEL TO A HYDRODYNAMIC DESCRIPTION

Here, we coarse grain the microscopic model for active screws [Eqs. (1)–(3)], to derive the hydrodynamic equations describing their collective behavior. We repeat the Langevin equations of motion here for convenience:

$$\dot{\phi}_i = \omega\Phi_i(t) + \frac{\tau_i}{\xi_s}, \quad (\text{C1})$$

$$\frac{d\mathbf{r}_i}{dt} = \ell_{\parallel}\dot{\phi}_i\hat{\mathbf{n}}_i - \ell_{\perp}\dot{\phi}_i\boldsymbol{\epsilon} \cdot \hat{\mathbf{n}}_i + \frac{\mathbf{F}_i}{\xi_t}, \quad (\text{C2})$$

$$\frac{d\theta_i}{dt} = \frac{\Gamma_i}{\xi_r} + \eta_i^r(t). \quad (\text{C3})$$

The meaning of the different terms is explained in Sec. II. To perform the coarse graining, we follow the derivations in Refs. [55,60] and extend them to include the spinning-rate variable specific to active screws.

1. Eliminating the equation of motion for the spinning rate

As explained in Sec. III, before starting the coarse graining, we eliminate Eq. (C1) by introducing it into Eq. (C2). This substitution, however, does not eliminate the spinning rate $\dot{\phi}_i$ as a degree of freedom, as $\dot{\phi}_i$ is still present in the spin torque transfer τ_i . In addition to the interaction term represented by τ_i , Eq. (C1) features the stochastic active driving term $\omega\Phi_i(t)$, which captures stochastic reversals of the self-propulsion direction. Such reversals were shown to give rise to an effective rotational diffusivity $D_r^{\text{eff}} = D_r + 2f_{\text{rev}}$, where f_{rev} is the average reversal frequency [54]. Therefore, after eliminating Eq. (C1), the effective Langevin equations of motion for active screws reduce to

$$\frac{d\mathbf{r}_i}{dt} = \left[\omega + \frac{\tau_i}{\xi_s} \right] [\ell_{\parallel}\hat{\mathbf{n}}_i - \ell_{\perp}\boldsymbol{\epsilon} \cdot \hat{\mathbf{n}}_i] + \frac{\mathbf{F}_i}{\xi_t}, \quad (\text{C4})$$

$$\frac{d\theta_i}{dt} = \frac{\Gamma_i}{\xi_r} + \eta_i^{r,\text{eff}}(t), \quad (\text{C5})$$

where $\langle \eta_i^{r,\text{eff}}(t) \eta_j^{r,\text{eff}}(t') \rangle = 2D_r^{\text{eff}} \delta(t - t') \delta_{ij}$.

2. Smoluchowski equation and the BBGKY hierarchy

The behavior of the system encoded in the set of coupled Langevin equations (C4) and (C5) can be equivalently described by the Smoluchowski equation for the N -particle distribution function $\Psi_N(\mathbf{r}_1, \hat{\mathbf{n}}_1, \phi_1, \dots, \mathbf{r}_N, \hat{\mathbf{n}}_N, \phi_N; t)$, which is the probability density of finding the N particles at positions $\mathbf{r}_1, \dots, \mathbf{r}_N$ with orientations $\hat{\mathbf{n}}_1, \dots, \hat{\mathbf{n}}_N$ and spinning at rates $\phi_1, \dots, \phi_N$ at time t :

$$\partial_t \Psi_N = - \sum_{i=1}^N [\nabla_i \cdot \mathbf{J}_{t,i} + \partial_{\theta_i} J_{r,i}]. \quad (\text{C6})$$

Here, $\mathbf{J}_t$ and J_r are the translational and rotational probability currents, respectively, given by

$$\mathbf{J}_{t,i} = \left\{ \left[\omega + \frac{\tau_i}{\xi_s} \right] [\ell_{\parallel} \hat{\mathbf{n}}_i - \ell_{\perp} \boldsymbol{\epsilon} \cdot \hat{\mathbf{n}}_i] + \frac{\mathbf{F}_i}{\xi_t} \right\} \Psi_N, \quad (\text{C7a})$$

$$J_{r,i} = \frac{\Gamma_i}{\xi_r} \Psi_N - D_r^{\text{eff}} \partial_{\theta_i} \Psi_N. \quad (\text{C7b})$$

Note that the two-dimensional particle orientation $\hat{\mathbf{n}}_i$ is given in terms of the angle θ_i as $\hat{\mathbf{n}}_i = (\cos \theta_i, \sin \theta_i)^T$.

Integrating over the positions, orientations, and spinning rates of all particles but one, we obtain an equation for the

one-particle distribution function $\Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1; t)$:

$$\begin{aligned} \partial_t \Psi_1 = & -\nabla_1 \cdot [\omega(\ell_{\parallel} \hat{\mathbf{n}}_1 - \ell_{\perp} \boldsymbol{\epsilon} \cdot \hat{\mathbf{n}}_1) \Psi_1] \\ & - \nabla_1 \cdot \left[(\ell_{\parallel} \hat{\mathbf{n}}_1 - \ell_{\perp} \boldsymbol{\epsilon} \cdot \hat{\mathbf{n}}_1) \frac{\tau_{\text{int}}}{\xi_s} \right] - \nabla_1 \cdot \frac{\mathbf{F}_{\text{int}}}{\xi_t} \\ & - \partial_{\theta_1} \frac{\Gamma_{\text{int}}}{\xi_r} + D_r^{\text{eff}} \partial_{\theta_1}^2 \Psi_1. \end{aligned} \quad (\text{C8})$$

Here, $\mathbf{F}_{\text{int}}$, Γ_{int} , and τ_{int} are the collective force, orientational torque, and spin torque, respectively, which encode the effects of interactions on particle 1. For pairwise interactions, they can be expressed in terms of the two-particle distribution function $\Psi_2(\mathbf{r}_1, \theta_1, \dot{\phi}_1, \mathbf{r}_2, \theta_2, \dot{\phi}_2; t)$ as

$$\mathbf{F}_{\text{int}}(\mathbf{r}_1, \theta_1, \dot{\phi}_1; t) = \int d^2 \mathbf{r}' d\theta' d\dot{\phi}' \mathbf{F}(\mathbf{r}' - \mathbf{r}_1, \theta' - \theta_1) \Psi_2(\mathbf{r}_1, \theta_1, \dot{\phi}_1, \mathbf{r}', \theta', \dot{\phi}'; t), \quad (\text{C9a})$$

$$\Gamma_{\text{int}}(\mathbf{r}_1, \theta_1, \dot{\phi}_1; t) = \int d^2 \mathbf{r}' d\theta' d\dot{\phi}' \Gamma(\mathbf{r}' - \mathbf{r}_1, \theta' - \theta_1) \Psi_2(\mathbf{r}_1, \theta_1, \dot{\phi}_1, \mathbf{r}', \theta', \dot{\phi}'; t), \quad (\text{C9b})$$

$$\tau_{\text{int}}(\mathbf{r}_1, \theta_1, \dot{\phi}_1; t) = \int d^2 \mathbf{r}' d\theta' d\dot{\phi}' \tau(\mathbf{r}' - \mathbf{r}_1, \theta' - \theta_1, \dot{\phi}' + \dot{\phi}_1) \Psi_2(\mathbf{r}_1, \theta_1, \dot{\phi}_1, \mathbf{r}', \theta', \dot{\phi}'; t). \quad (\text{C9c})$$

Here, $\mathbf{F}(\mathbf{r}, \theta)$, $\Gamma(\mathbf{r}, \theta)$, and $\tau(\mathbf{r}, \theta, \dot{\phi})$ are the force, orientation torque, and spin torque of interaction between the two particles. These quantities depend on the relative coordinates $\mathbf{r} = \mathbf{r}' - \mathbf{r}_1$, $\theta = \theta' - \theta_1$, and $\dot{\phi} = \dot{\phi}' + \dot{\phi}_1$ of the interacting pair. With the assumptions discussed in Sec. II, the dependencies of the interaction forces and torques on the relative coordinates reduce to

$$\mathbf{F}(\mathbf{r}, \theta) = -F_r(r) \cos \theta \hat{\mathbf{r}}, \quad (\text{C10a})$$

$$\Gamma(\mathbf{r}, \theta) = \Gamma_r(r) \sin(2\theta), \quad (\text{C10b})$$

$$\tau(\mathbf{r}, \theta, \dot{\phi}) = \tau_r(r) \dot{\phi} \cos \theta, \quad (\text{C10c})$$

where the functions $F_r(r)$, $\Gamma_r(r)$, and $\tau_r(r)$ capture unspecified radial dependencies of the interactions, with $r = |\mathbf{r}|$ being the distance between the interacting particles.

With the collective force and torques given by Eq. (C9), Eq. (C8) is an integro-differential equation for Ψ_1 that involves Ψ_2 . Therefore, Eq. (C8) is the first equation in the BBGKY hierarchy. To truncate the hierarchy, we decompose Ψ_2 as

$$\begin{aligned} \Psi_2(\mathbf{r}_1, \theta_1, \dot{\phi}_1, \mathbf{r}', \theta', \dot{\phi}'; t) &= \Psi_1(\mathbf{r}', \theta', \dot{\phi}'; t) \\ &\times g(\mathbf{r}', \theta', \dot{\phi}' | \mathbf{r}_1, \theta_1, \dot{\phi}_1; t) \Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1; t). \end{aligned} \quad (\text{C11})$$

Here, $\Psi_2(\mathbf{r}_1, \theta_1, \dot{\phi}_1, \mathbf{r}', \theta', \dot{\phi}'; t)$ is the density of particle pairs with one particle with position $\mathbf{r}_1$, orientation θ_1 , and spinning

rate $\dot{\phi}_1$, and another particle with position $\mathbf{r}'$, orientation θ' , and spinning rate $\dot{\phi}'$ at time t . Respectively, g is the dimensionless pair distribution function that encodes the conditional probability of finding a particle with position $\mathbf{r}'$, orientation θ' , and spinning rate $\dot{\phi}'$ given that another particle has position $\mathbf{r}_1$, orientation θ_1 , and spinning rate $\dot{\phi}_1$. Introducing this decomposition into Eq. (C8) allows us to express it as a closed equation for Ψ_1 , hence closing the hierarchy. This closure goes beyond the molecular chaos approximation, as it keeps information about pair correlations in the pair distribution function g .

In homogeneous steady states, the probability distributions are time independent, and the pair correlations do not depend on the coordinates of a given particle but only on the relative coordinates of particle pairs, defined just above Eq. (C10). Hence, we express g in terms of the distance r between particles, the angle φ formed between the interparticle distance vector $\mathbf{r}$ and the orientation vector $\hat{\mathbf{n}}_1$ of particle 1 (defined by $\hat{\mathbf{n}}_1 \cdot \mathbf{r} = r \cos \varphi$), the relative orientation θ , and the relative spinning rate $\dot{\phi}$. Therefore, in homogeneous steady states like the isotropic and nematic states of active screws that we analyze, we have

$$g(\mathbf{r}', \theta', \dot{\phi}' | \mathbf{r}_1, \theta_1, \dot{\phi}_1; t) = g(r, \varphi, \theta, \dot{\phi}). \quad (\text{C12})$$

With this decomposition, and changing the integration variables to the relative coordinates, the collective force and torques [Eq. (C9)] are expressed as

$$\mathbf{F}_{\text{int}}(\mathbf{r}_1, \theta_1, \dot{\phi}_1) = \Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1) \int d^2 \mathbf{r} d\theta d\dot{\phi} \mathbf{F}(\mathbf{r}, \theta) \Psi_1(\mathbf{r} + \mathbf{r}_1, \theta + \theta_1, \dot{\phi} - \dot{\phi}_1) g(r, \varphi, \theta, \dot{\phi}), \quad (\text{C13a})$$

$$\Gamma_{\text{int}}(\mathbf{r}_1, \theta_1, \dot{\phi}_1) = \Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1) \int d^2 \mathbf{r} d\theta d\dot{\phi} \Gamma(\mathbf{r}, \theta) \Psi_1(\mathbf{r} + \mathbf{r}_1, \theta + \theta_1, \dot{\phi} - \dot{\phi}_1) g(r, \varphi, \theta, \dot{\phi}), \quad (\text{C13b})$$

$$\tau_{\text{int}}(\mathbf{r}_1, \theta_1, \dot{\phi}_1) = \Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1) \int d^2 \mathbf{r} d\theta d\dot{\phi} \tau(\mathbf{r}, \theta, \dot{\phi}) \Psi_1(\mathbf{r} + \mathbf{r}_1, \theta + \theta_1, \dot{\phi} - \dot{\phi}_1) g(r, \varphi, \theta, \dot{\phi}). \quad (\text{C13c})$$

3. Fourier and gradient expansions

The one-particle distribution function Ψ_1 in the integrand of Eq. (C13) introduces nonlocal dependencies in $\mathbf{r}_1$, θ_1 , and $\dot{\phi}_1$. To derive local hydrodynamic equations, we perform a Fourier expansion on the orientation angle,

$$\Psi_1(\mathbf{r}', \theta', \dot{\phi}') = \frac{1}{2\pi} \sum_{k=0}^{\infty} e^{-ik\theta'} \tilde{\Psi}_{1,k}(\mathbf{r}', \dot{\phi}'), \quad (\text{C14})$$

and then a gradient expansion of the Fourier components on both the position and the spinning rate,

$$\begin{aligned} \tilde{\Psi}_{1,k}(\mathbf{r}', \dot{\phi}') &\approx \tilde{\Psi}_{1,k}(\mathbf{r}_1, \dot{\phi}_1) + (\mathbf{r}' - \mathbf{r}_1) \cdot \nabla_{\mathbf{r}'} \tilde{\Psi}_{1,k}(\mathbf{r}_1, \dot{\phi}_1) \\ &+ (\dot{\phi}' - \dot{\phi}_1) \partial_{\dot{\phi}'} \tilde{\Psi}_{1,k}(\mathbf{r}_1, \dot{\phi}_1). \end{aligned} \quad (\text{C15})$$

The arguments in these expressions relate to those of Ψ_1 in the integrand of Eq. (C13) via the transformations to the relative coordinates: $\mathbf{r} = \mathbf{r}' - \mathbf{r}_1$, $\theta = \theta' - \theta_1$, and $\dot{\phi} = \dot{\phi}' + \dot{\phi}_1$.

a. Zeroth-order contributions

Based on this gradient expansion, we now obtain first the zeroth-order and then the first-order contributions to the collective interaction force and torques in Eq. (C13). The interaction force is a vector, which we take to be along the interparticle distance axis $\hat{\mathbf{r}}$, as in Eq. (C10a). We then decompose it into components parallel and perpendicular to the orientation of particle 1: $\hat{\mathbf{r}} = \cos \varphi \hat{\mathbf{n}}_1 + \sin \varphi \hat{\mathbf{t}}_1$, where $\hat{\mathbf{t}}_1$ is unit vector transverse to $\hat{\mathbf{n}}_1$, which thus fulfills $\hat{\mathbf{t}}_1 \cdot \hat{\mathbf{n}}_1 = 0$. Using this decomposition in Eq. (C13a), the zeroth-order contributions of Eq. (C13) are given by

$$F_{\text{int},\parallel}^{(0)}(\mathbf{r}_1, \theta_1, \dot{\phi}_1) = -\Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1) \frac{1}{2\pi} \sum_{k=0}^{\infty} e^{-ik\theta_1} \tilde{\Psi}_{1,k}(\mathbf{r}_1, \dot{\phi}_1) \zeta_{0,k}^{\parallel}, \quad (\text{C16a})$$

$$F_{\text{int},\perp}^{(0)}(\mathbf{r}_1, \theta_1, \dot{\phi}_1) = -\Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1) \frac{1}{2\pi} \sum_{k=0}^{\infty} e^{-ik\theta_1} \tilde{\Psi}_{1,k}(\mathbf{r}_1, \dot{\phi}_1) \zeta_{0,k}^{\perp}, \quad (\text{C16b})$$

$$\Gamma_{\text{int}}^{(0)}(\mathbf{r}_1, \theta_1, \dot{\phi}_1) = \Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1) \frac{1}{2\pi} \sum_{k=0}^{\infty} e^{-ik\theta_1} \tilde{\Psi}_{1,k}(\mathbf{r}_1, \dot{\phi}_1) \gamma_{0,k}, \quad (\text{C16c})$$

$$\tau_{\text{int}}^{(0)}(\mathbf{r}_1, \theta_1, \dot{\phi}_1) = \Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1) \frac{1}{2\pi} \sum_{k=0}^{\infty} e^{-ik\theta_1} \tilde{\Psi}_{1,k}(\mathbf{r}_1, \dot{\phi}_1) \tau_{0,k}, \quad (\text{C16d})$$

where we have defined the coefficients

$$\zeta_{0,k}^{\parallel} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} F(r, \varphi, \theta) g(r, \varphi, \theta, \dot{\phi}) \cos \varphi e^{-ik\theta}, \quad (\text{C17a})$$

$$\zeta_{0,k}^{\perp} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} F(r, \varphi, \theta) g(r, \varphi, \theta, \dot{\phi}) \sin \varphi e^{-ik\theta}, \quad (\text{C17b})$$

$$\gamma_{0,k} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} \Gamma(r, \varphi, \theta) g(r, \varphi, \theta, \dot{\phi}) e^{-ik\theta}, \quad (\text{C17c})$$

$$\tau_{0,k} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} \tau(r, \varphi, \theta, \dot{\phi}) g(r, \varphi, \theta, \dot{\phi}) e^{-ik\theta}. \quad (\text{C17d})$$

b. First-order contributions

We now obtain the first-order contributions to the collective interaction force and torques in Eq. (C13). We proceed as for the zeroth-order terms, except that we now also split the spatial gradients in components parallel and perpendicular to $\hat{\mathbf{n}}_1$. Thus, we obtain

$$F_{\text{int},\parallel}^{(1)}(\mathbf{r}_1, \theta_1, \dot{\phi}_1) = -\Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1) \frac{1}{2\pi} \sum_{k=0}^{\infty} e^{-ik\theta_1} [\zeta_{1,k,\parallel}^{\parallel} \nabla_{\parallel} + \zeta_{1,k,\perp}^{\parallel} \nabla_{\perp} + \zeta_{1,k,\phi}^{\parallel} \partial_{\dot{\phi}}] \tilde{\Psi}_{1,k}(\mathbf{r}_1, \dot{\phi}_1), \quad (\text{C18a})$$

$$F_{\text{int},\perp}^{(1)}(\mathbf{r}_1, \theta_1, \dot{\phi}_1) = -\Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1) \frac{1}{2\pi} \sum_{k=0}^{\infty} e^{-ik\theta_1} [\zeta_{1,k,\parallel}^{\perp} \nabla_{\parallel} + \zeta_{1,k,\perp}^{\perp} \nabla_{\perp} + \zeta_{1,k,\phi}^{\perp} \partial_{\dot{\phi}}] \tilde{\Psi}_{1,k}(\mathbf{r}_1, \dot{\phi}_1), \quad (\text{C18b})$$

$$\Gamma_{\text{int}}^{(1)}(\mathbf{r}_1, \theta_1, \dot{\phi}_1) = \Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1) \frac{1}{2\pi} \sum_{k=0}^{\infty} e^{-ik\theta_1} [\gamma_{1,k,\parallel} \nabla_{\parallel} + \gamma_{1,k,\perp} \nabla_{\perp} + \gamma_{1,k,\phi} \partial_{\dot{\phi}}] \tilde{\Psi}_{1,k}(\mathbf{r}_1, \dot{\phi}_1), \quad (\text{C18c})$$

$$\tau_{\text{int}}^{(1)}(\mathbf{r}_1, \theta_1, \dot{\phi}_1) = \Psi_1(\mathbf{r}_1, \theta_1, \dot{\phi}_1) \frac{1}{2\pi} \sum_{k=0}^{\infty} e^{-ik\theta_1} [\tau_{1,k,\parallel} \nabla_{\parallel} + \tau_{1,k,\perp} \nabla_{\perp} + \tau_{1,k,\phi} \partial_{\dot{\phi}}] \tilde{\Psi}_{1,k}(\mathbf{r}_1, \dot{\phi}_1), \quad (\text{C18d})$$

where we have defined the coefficients

$$\zeta_{1,k,\parallel}^{\parallel} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} F(r, \varphi, \theta) g(r, \varphi, \theta, \dot{\phi}) r \cos^2 \varphi e^{-ik\theta}, \quad (\text{C19a})$$

$$\zeta_{1,k,\perp}^{\parallel} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} F(r, \varphi, \theta) g(r, \varphi, \theta, \dot{\phi}) r \cos \varphi \sin \varphi e^{-ik\theta}, \quad (\text{C19b})$$

$$\zeta_{1,k,\dot{\phi}}^{\parallel} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} F(r, \varphi, \theta) g(r, \varphi, \theta, \dot{\phi}) \dot{\phi} \cos \varphi e^{-ik\theta}, \quad (\text{C19c})$$

$$\zeta_{1,k,\parallel}^{\perp} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} F(r, \varphi, \theta) g(r, \varphi, \theta, \dot{\phi}) r \sin \varphi \cos \varphi e^{-ik\theta}, \quad (\text{C19d})$$

$$\zeta_{1,k,\perp}^{\perp} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} F(r, \varphi, \theta) g(r, \varphi, \theta, \dot{\phi}) r \sin^2 \varphi e^{-ik\theta}, \quad (\text{C19e})$$

$$\zeta_{1,k,\dot{\phi}}^{\perp} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} F(r, \varphi, \theta) g(r, \varphi, \theta, \dot{\phi}) \dot{\phi} \sin \varphi e^{-ik\theta}, \quad (\text{C19f})$$

$$\gamma_{1,k,\parallel} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} \Gamma(r, \varphi, \theta) g(r, \varphi, \theta, \dot{\phi}) r \cos \varphi e^{-ik\theta}, \quad (\text{C19g})$$

$$\gamma_{1,k,\perp} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} \Gamma(r, \varphi, \theta) g(r, \varphi, \theta, \dot{\phi}) r \sin \varphi e^{-ik\theta}, \quad (\text{C19h})$$

$$\gamma_{1,k,\dot{\phi}} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} \Gamma(r, \varphi, \theta) g(r, \varphi, \theta, \dot{\phi}) \dot{\phi} e^{-ik\theta}, \quad (\text{C19i})$$

$$\tau_{1,k,\parallel} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} \tau(r, \varphi, \theta, \dot{\phi}) g(r, \varphi, \theta, \dot{\phi}) r \cos \varphi e^{-ik\theta}, \quad (\text{C19j})$$

$$\tau_{1,k,\perp} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} \tau(r, \varphi, \theta, \dot{\phi}) g(r, \varphi, \theta, \dot{\phi}) r \sin \varphi e^{-ik\theta}, \quad (\text{C19k})$$

$$\tau_{1,k,\dot{\phi}} \equiv \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \int_{-\infty}^{\infty} d\dot{\phi} \tau(r, \varphi, \theta, \dot{\phi}) g(r, \varphi, \theta, \dot{\phi}) \dot{\phi} e^{-ik\theta}. \quad (\text{C19l})$$

Here, as in the zeroth-order terms, the $\parallel$ and $\perp$ superscripts refer to the components of the collective force $\mathbf{F}_{\text{int}}$ parallel and perpendicular to $\hat{\mathbf{n}}_1$. Respectively, the $\parallel$, $\perp$, and $\dot{\phi}$ subscripts refer to the components of the spatial gradients parallel and perpendicular to $\hat{\mathbf{n}}_1$, $\nabla_{\parallel}$, and $\nabla_{\perp}$, and to the spinning-rate gradient $\partial_{\dot{\phi}}$ in Eq. (C18).

4. Moment hierarchy and hydrodynamic equations

To complete the coarse graining of the microscopic model, we define continuum fields as the angular moments of the one-particle distribution function Ψ_1 . For example, the zeroth moment corresponds to the density field $\rho(\mathbf{r}, t)$, the first moment corresponds to the polarization density $\mathbf{p}(\mathbf{r}, t)$, and the second moment is related to the nematic order-parameter tensor density $\mathbf{Q}(\mathbf{r}, t)$:

$$\rho(\mathbf{r}, t) = \int \Psi_1(\mathbf{r}, \theta, \dot{\phi}, t) d\theta d\dot{\phi}, \quad (\text{C20a})$$

$$p_{\alpha}(\mathbf{r}, t) = \int n_{\alpha} \Psi_1(\mathbf{r}, \theta, \dot{\phi}, t) d\theta d\dot{\phi}, \quad (\text{C20b})$$

$$Q_{\alpha\beta}(\mathbf{r}, t) = \int \left[n_{\alpha} n_{\beta} - \frac{1}{2} \delta_{\alpha\beta} \right] \Psi_1(\mathbf{r}, \theta, \dot{\phi}, t) d\theta d\dot{\phi}. \quad (\text{C20c})$$

We can then obtain hydrodynamic equations for each of these fields by taking the corresponding moment of the Smoluchowski equation [Eq. (C8)] for the one-particle distribution Ψ_1 . We will obtain hydrodynamic equations in this way in the following two sections for the isotropic and the nematic states, respectively.

APPENDIX D: ISOTROPIC-NEMATIC TRANSITION

Here, we use our coarse-graining approach to predict the onset of nematic order in our system. In Fig. 3, we compare the prediction obtained here with the numerical results from our simulations, described in Appendixes A and B. Given that spin torque transfer has no macroscopic consequences for uniform phases, here we ignore the spin-rate degree of freedom. Thus, our calculation considers self-propelled rolling particles that interact both via central forces and via orientation torques.

Following Refs. [55,62], to determine a transition between uniform phases, we will consider Eq. (C8) to lowest order in gradients:

$$\partial_t \Psi_1 = -\partial_{\theta_1} \frac{\Gamma_{\text{int}}}{\xi_r} + D_r^{\text{eff}} \partial_{\theta_1}^2 \Psi_1. \quad (\text{D1})$$

Next, we expand the distribution function in angular Fourier components as

$$\Psi_1(\mathbf{r}', \theta') = \frac{1}{2\pi} \sum_{k=0}^{\infty} e^{-ik\theta'} \tilde{\Psi}_{1,k}(\mathbf{r}'). \quad (\text{D2})$$

In terms of the Fourier components, Eq. (D1) reads

$$\partial_t \tilde{\Psi}_{1,k} = \frac{ik}{2\pi \xi_r} \sum_{m=0}^{\infty} \tilde{\Psi}_{1,m} \gamma_{0,m} \tilde{\Psi}_{1,k-m} - D_r^{\text{eff}} k^2 \tilde{\Psi}_{1,k}, \quad (\text{D3})$$

where the torque coefficients $\gamma_{0,m}$, first introduced in Eq. (C17), are given here by

$$\gamma_{0,m} = \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \Gamma(r, \varphi, \theta) g(r, \varphi, \theta) e^{-im\theta}. \quad (\text{D4})$$

We next introduce the correspondence of the hydrodynamic fields, defined in Eq. (C20), with the Fourier components of the one-particle distribution function Ψ_1 :

$$\rho(\mathbf{r}, t) = \tilde{\Psi}_{1,0}(\mathbf{r}, t), \quad (\text{D5a})$$

$$\mathbf{p}(\mathbf{r}, t) = \begin{pmatrix} \text{Re} \tilde{\Psi}_{1,1}(\mathbf{r}, t) \\ \text{Im} \tilde{\Psi}_{1,1}(\mathbf{r}, t) \end{pmatrix}, \quad (\text{D5b})$$

$$\mathbf{Q}(\mathbf{r}, t) = \frac{1}{2} \begin{pmatrix} \text{Re} \tilde{\Psi}_{1,2}(\mathbf{r}, t) & \text{Im} \tilde{\Psi}_{1,2}(\mathbf{r}, t) \\ \text{Im} \tilde{\Psi}_{1,2}(\mathbf{r}, t) & -\text{Re} \tilde{\Psi}_{1,2}(\mathbf{r}, t) \end{pmatrix}. \quad (\text{D5c})$$

Based on these correspondences, we derive the dynamics of the nematic order-parameter tensor $\mathbf{Q}$ by taking the $k = 2$ Fourier mode of Eq. (D3), which gives

$$\begin{aligned} \partial_t \tilde{\Psi}_{1,2} = & \frac{2i}{2\pi \xi_r} (\tilde{\Psi}_{1,0} \gamma_{0,0} \tilde{\Psi}_{1,2} + \tilde{\Psi}_{1,1} \gamma_{0,1} \tilde{\Psi}_{1,1} \\ & + \tilde{\Psi}_{1,2} \gamma_{0,2} \tilde{\Psi}_{1,0}) - 4D_r \tilde{\Psi}_{1,2}, \end{aligned} \quad (\text{D6})$$

where we have replaced $D_r^{\text{eff}} \rightarrow D_r$ to account for the fact that reversal events do not impact nematic order, as discussed in Sec. IV.

We now use the specific orientation torques in the simulations, given in Eq. (A2), as well as the global chiral symmetry in the simulations, which implies $g(r, -\varphi, -\theta) = g(r, \varphi, \theta)$. Introducing these specifications in Eq. (D4), we obtain the coefficients γ in Eq. (D6), which are given by

$$\gamma_{0,0} = 0, \quad (\text{D7a})$$

$$\gamma_{0,1} = -i \int_0^{r_r} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \Gamma_0 \sin(2\theta) \sin \theta g(r, \varphi, \theta), \quad (\text{D7b})$$

$$\gamma_{0,2} = -i \int_0^{r_r} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \Gamma_0 \sin^2(2\theta) g(r, \varphi, \theta). \quad (\text{D7c})$$

With these results, and defining $\gamma_1 \equiv i\gamma_{0,1}$ and $\gamma_2 \equiv i\gamma_{0,2}$ for notation convenience, we recast Eq. (D6) into the following dynamics for the nematic order-parameter tensor:

$$\partial_t \mathbf{Q} = \frac{1}{\pi \xi_r} (\gamma_1 \mathbf{p} \mathbf{p} + \gamma_2 \rho \mathbf{Q}) - 4D_r \mathbf{Q} \quad (\text{D8})$$

to lowest order in gradients. For states with zero net polarity ($\mathbf{p} = \mathbf{0}$), like the ones considered in our simulations, this result further simplifies to

$$\partial_t \mathbf{Q} = a_Q[\rho] \mathbf{Q}, \quad (\text{D9})$$

where

$$a_Q[\rho] = \frac{\gamma_2}{\pi \xi_r} \rho - 4D_r \quad (\text{D10})$$

is the growth rate of the nematic order, as given in Eq. (5). If $a < 0$, the isotropic state with $\mathbf{Q} = \mathbf{0}$ is stable. If $a > 0$, it is unstable to the appearance of nematic order. Thus, the condition $a_Q[\rho] = 0$ determines the phase boundary for the isotropic-nematic transition.

To predict this phase boundary, we measure the pair distribution function $g(r, \varphi, \theta)$ from our simulations, and we use it to calculate γ_2 via the following integral:

$$\gamma_2 = \int_0^{r_r} dr r \int_0^{2\pi} d\varphi \int_0^{2\pi} d\theta \Gamma_0 \sin^2(2\theta) g(r, \varphi, \theta). \quad (\text{D11})$$

Performing this calculation for simulations at different values of the self-propulsion speed v_0 and the area fraction ϕ_0 , we evaluate the growth rate in Eq. (D10), and we look for the values of v_0 and ϕ_0 at which it crosses zero. These crossing values give the phase boundary that we plot in Fig. 3. These theoretical results capture the emergence of nematic order observed in our simulations.

APPENDIX E: HYDRODYNAMIC EQUATIONS FOR THE CHIRAL NEMATIC STATE

In this Appendix, we use the coarse-graining results of Appendix C to obtain the hydrodynamic equations for the nematic, possibly also chiral, state.

To this end, we first simplify the expressions of the coefficients in Eqs. (C17) and (C19) through three assumptions:

(1) We introduce the specific forms of the interaction force and torques given in Eq. (C10).

(2) We assume that the entire system is nonchiral, as half of the screws will spin in one sense and half of the screws in the other. Hence, the pair correlation function has to be invariant upon chiral transformations, i.e., simultaneous change of sign of the angles φ and θ , $g(r, -\varphi, -\theta, \dot{\phi}) = g(r, \varphi, \theta, \dot{\phi})$, and upon change of sign of the spinning rate $\dot{\phi}$, $g(r, \varphi, \theta, -\dot{\phi}) = g(r, \varphi, \theta, \dot{\phi})$.

(3) We consider the system of active screws to be deep in the nematic state. In this state, the orientation differences between pairs of particles are very small and, hence, the pair correlation function is sharply peaked around $\theta = 0$: $g(r, \varphi, \theta, \dot{\phi}) \approx g_{\text{nem}}(r, \varphi, \dot{\phi}) \delta(\theta)$.

With these assumptions, for the zeroth-order coefficients, we get that $\zeta_{0,k}^{\parallel}$ does not vanish and it is given by

$$\zeta_0 = \int_0^{\infty} dr r \int_0^{2\pi} d\varphi \int_{-\infty}^{\infty} d\dot{\phi} F_r(r) g_{\text{nem}}(r, \varphi, \dot{\phi}) \cos \varphi, \quad (\text{E1})$$

Here, we have renamed $\zeta_{0,k}^{\parallel} \rightarrow \zeta_0$ using that this coefficient is now independent of k . The other coefficients in Eq. (C17) vanish: $\zeta_{0,k}^{\perp} = 0$, $\gamma_{0,k} = 0$, and $\tau_{0,k} = 0$. Therefore, with these

specifications for the nematic state, the collective force and torques at zeroth order in the gradient expansion, given in Eq. (C16), reduce to

$$\mathbf{F}_{\text{int}}^{(0)} = -\Psi_1^2 \zeta_0 \hat{\mathbf{n}}_1, \quad (\text{E2a})$$

$$\Gamma_{\text{int}}^{(0)} = 0, \quad (\text{E2b})$$

$$\tau_{\text{int}}^{(0)} = 0. \quad (\text{E2c})$$

Next, we simplify the expressions of the first-order coefficients [Eq. (C19)]. We obtain

$$\zeta_{1,\parallel}^{\parallel} = \int_0^\infty dr \int_0^{2\pi} d\varphi \int_{-\infty}^\infty d\dot{\phi} F_r(r) g_{\text{nem}}(r, \varphi, \dot{\phi}) r^2 \cos^2 \varphi, \quad (\text{E3a})$$

$$\zeta_{1,\perp}^{\perp} = \int_0^\infty dr \int_0^{2\pi} d\varphi \int_{-\infty}^\infty d\dot{\phi} F_r(r) g_{\text{nem}}(r, \varphi, \dot{\phi}) r^2 \sin^2 \varphi, \quad (\text{E3b})$$

$$\tau_{1,\phi} = \int_0^\infty dr \int_0^{2\pi} d\varphi \int_{-\infty}^\infty d\dot{\phi} \tau_r(r) g_{\text{nem}}(r, \varphi, \dot{\phi}) r \dot{\phi}^2, \quad (\text{E3c})$$

where we have dropped the subindex k because these coefficients are now independent of the angular mode number. The rest of coefficients in Eq. (C19) vanish. For simplicity, following previous work [60], we replace the integrals in the expressions of $\zeta_{1,k,\parallel}^{\parallel}$ and $\zeta_{1,k,\perp}^{\perp}$ by their average, thus replacing both $\zeta_{1,k,\parallel}^{\parallel}$ and $\zeta_{1,k,\perp}^{\perp}$ by

$$\zeta_1 \equiv \frac{1}{2} \int_0^\infty dr \int_0^{2\pi} d\varphi \int_{-\infty}^\infty d\dot{\phi} F_r(r) g_{\text{nem}}(r, \varphi, \dot{\phi}) r^2. \quad (\text{E4})$$

Thus, the collective force and torques at first order in the gradient expansion, specified for the nematic state, are given by

$$\mathbf{F}_{\text{int}}^{(1)} = -\Psi_1 \zeta_1 \nabla \Psi_1, \quad (\text{E5a})$$

$$\Gamma_{\text{int}}^{(1)} = 0, \quad (\text{E5b})$$

$$\tau_{\text{int}}^{(1)} = \Psi_1 \tau_{1,\phi} \partial_\phi \Psi_1. \quad (\text{E5c})$$

Putting together the zeroth- and first-order terms, the collective force and torques representing the effects of interactions on a reference particle in the nematic state read

$$\mathbf{F}_{\text{int}} = -\Psi_1^2 \zeta_0 \hat{\mathbf{n}}_1 - \Psi_1 \zeta_1 \nabla \Psi_1, \quad (\text{E6a})$$

$$\Gamma_{\text{int}} = 0, \quad (\text{E6b})$$

$$\tau_{\text{int}} = \Psi_1 \tau_{1,\phi} \partial_\phi \Psi_1. \quad (\text{E6c})$$

Finally, introducing these results in the Smoluchowski equation [Eq. (C8)] and taking the orientational moments as

introduced in Appendix C4, we obtain the following equations for the density, polarity, and nematic order-parameter fields:

$$\partial_t \rho = -\nabla \cdot \mathbf{J}, \quad \mathbf{J} = v_{\parallel} [\rho] \mathbf{p} - v_{\perp} \boldsymbol{\epsilon} \cdot \mathbf{p} - \zeta_1 \rho \nabla \rho, \quad (\text{E7a})$$

$$\begin{aligned} \partial_t \mathbf{p} = & -\nabla \cdot (v_{\parallel} [\rho] \mathbf{Q}) - \frac{1}{2} \nabla (v_{\parallel} [\rho] \rho) + \nabla \cdot (v_{\perp} \boldsymbol{\epsilon} \cdot \mathbf{Q}) \\ & + \frac{1}{2} \boldsymbol{\epsilon} \cdot \nabla (v_{\perp} \rho) + \nabla \cdot (\zeta_1 \mathbf{p} \nabla \rho) - D_r^{\text{eff}} \mathbf{p}, \end{aligned} \quad (\text{E7b})$$

which are quoted in Eqs. (7) and (8). To obtain these equations, when integrating the terms containing two factors of Ψ_1 in Eq. (E6a), we assume that they factor out and give rise to nonlinear terms in the hydrodynamic fields. For example, the term that goes like $\Psi_1^2 \hat{\mathbf{n}}_1$ in Eq. (E6a) coarse grains to a nonlinear term like $\rho \mathbf{p}$. The hydrodynamic equations [Eq. (E7)], together with the definitions

$$v_{\parallel} [\rho] = \omega \ell_{\parallel} - \zeta_0 \rho, \quad (\text{E8a})$$

$$v_{\perp} = \omega \ell_{\perp}, \quad (\text{E8b})$$

$$D_r^{\text{eff}} = D_r + 2f_{\text{rev}}, \quad (\text{E8c})$$

and the results for ζ_0 and ζ_1 in Eqs. (E1) and (E4), constitute the final result of our derivation for the nematic state. They specify the collective behavior of the system of active screws in terms of the parameters of their microscopic model, complemented with the pair correlation function in the nematic state, g_{nem} , needed to obtain ζ_0 and ζ_1 .

In general, the hydrodynamic equation for the k th moment involves the $(k+1)$ th moment, giving rise to a hierarchy of hydrodynamic equations. In Eq. (E7), the polarity equation contains the nematic order-parameter tensor $\mathbf{Q}$, which is the second-order orientational moment of Ψ_1 as defined in Eq. (C20).

APPENDIX F: FLOW FIELDS AROUND TOPOLOGICAL DEFECTS

We analyze the flows of *M. xanthus* bacteria around topological defects reported in Ref. [46] [Figs. 4(c) and 4(d)]. Using the procedure in Ref. [46], we fit the flows predicted by an incompressible active nematic, but now extended to include the chiral active stress $\zeta_c \boldsymbol{\epsilon} \cdot \mathbf{Q}$ [see Eq. (9)]. Setting other parameter values as in Ref. [46], we fit the achiral and chiral active stress coefficients, ζ and ζ_c , respectively, divided by the isotropic friction coefficient ξ_0 . We obtain $\zeta/\xi_0 = 0.46 \pm 0.01 \mu\text{m}^2/\text{min}$ and $\zeta_c = 0.05 \pm 0.01 \mu\text{m}^2/\text{min}$ for $+1/2$ defects, and $\zeta = 0.72 \pm 0.01 \mu\text{m}^2/\text{min}$ and $\zeta_c = -0.17 \pm 0.01 \mu\text{m}^2/\text{min}$ for $-1/2$ defects. These values are used to generate the theory plots in Fig. 4.

- [1] L. Meißner, L. Niese, and S. Diez, Helical motion and torque generation by microtubule motors, *Curr. Opin. Cell Biol.* **88**, 102367 (2024).
- [2] N. Wadhwa and H. C. Berg, Bacterial motility: Machinery and mechanisms, *Nat. Rev. Microbiol.* **20**, 161 (2022).
- [3] T. Mignot, J. W. Shaevitz, P. L. Hartzell, and D. R. Zusman, Evidence that focal adhesion complexes power bacterial gliding motility, *Science* **315**, 853 (2007).

- [4] R. Balagam, D. B. Litwin, F. Czerwinski, M. Sun, H. B. Kaplan, J. W. Shaevitz, and O. A. Igoshin, *Myxococcus xanthus* gliding motors are elastically coupled to the substrate as predicted by the focal adhesion model of gliding motility, *PLoS Comput. Biol.* **10**, e1003619 (2014).
- [5] S. T. Islam and T. Mignot, The mysterious nature of bacterial surface (gliding) motility: A focal adhesion-based mechanism in *Myxococcus xanthus*, *Semin. Cell Dev. Biol.* **46**, 143 (2015).

- [6] L. M. Faure, J.-B. Fiche, L. Espinosa, A. Ducret, V. Anantharaman, J. Luciano, S. Lhospice, S. T. Islam, J. Tréguier, M. Sotes, E. Kuru, M. S. Van Nieuwenhze, Y. V. Brun, O. Théodoly, L. Arvind, M. Nollmann, and T. Mignot, The mechanism of force transmission at bacterial focal adhesion complexes, *Nature (London)* **539**, 530 (2016).
- [7] D. Nakane, K. Sato, H. Wada, M. J. McBride, and K. Nakayama, Helical flow of surface protein required for bacterial gliding motility, *Proc. Natl. Acad. Sci. USA* **110**, 11145 (2013).
- [8] A. Shrivastava, P. P. Lele, and H. C. Berg, A rotary motor drives *Flavobacterium* gliding, *Curr. Biol.* **25**, 338 (2015).
- [9] A. Shrivastava and H. C. Berg, Towards a model for *Flavobacterium* gliding, *Curr. Opin. Microbiol.* **28**, 93 (2015).
- [10] A. Shrivastava, T. Roland, and H. C. Berg, The screw-like movement of a gliding bacterium is powered by spiral motion of cell-surface adhesins, *Biophys. J.* **111**, 1008 (2016).
- [11] T. H. Tan, A. Mietke, J. Li, Y. Chen, H. Higinbotham, P. J. Foster, S. Gokhale, J. Dunkel, and N. Fakhri, Odd dynamics of living chiral crystals, *Nature (London)* **607**, 287 (2022).
- [12] D. Cortese and K. Y. Wan, Control of helical navigation by three-dimensional flagellar beating, *Phys. Rev. Lett.* **126**, 088003 (2021).
- [13] K. Drescher, K. C. Leptos, I. Tuval, T. Ishikawa, T. J. Pedley, and R. E. Goldstein, Dancing *Volvox*: Hydrodynamic bound states of swimming algae, *Phys. Rev. Lett.* **102**, 168101 (2009).
- [14] L. Zhang, J. J. Abbott, L. Dong, B. E. Kratochvil, D. Bell, and B. J. Nelson, Artificial bacterial flagella: Fabrication and magnetic control, *Appl. Phys. Lett.* **94**, 064107 (2009).
- [15] A. Ghosh and P. Fischer, Controlled propulsion of artificial magnetic nanostructured propellers, *Nano Lett.* **9**, 2243 (2009).
- [16] S. Palagi and P. Fischer, Bioinspired microrobots, *Nat. Rev. Mater.* **3**, 113 (2018).
- [17] J. G. Gibbs and P. Fischer, Active colloidal microdrills, *Chem. Commun.* **51**, 4192 (2015).
- [18] E. Tjhung, M. E. Cates, and D. Marenduzzo, Contractile and chiral activities codetermine the helicity of swimming droplet trajectories, *Proc. Natl. Acad. Sci. USA* **114**, 4631 (2017).
- [19] L. N. Carenza, G. Gonnella, D. Marenduzzo, and G. Negro, Rotation and propulsion in 3D active chiral droplets, *Proc. Natl. Acad. Sci. USA* **116**, 22065 (2019).
- [20] C. Bechinger, R. Di Leonardo, H. Löwen, C. Reichhardt, G. Volpe, and G. Volpe, Active particles in complex and crowded environments, *Rev. Mod. Phys.* **88**, 045006 (2016).
- [21] B. Liebchen and D. Levis, Collective behavior of chiral active matter: Pattern formation and enhanced flocking, *Phys. Rev. Lett.* **119**, 058002 (2017).
- [22] B. Liebchen and D. Levis, Chiral active matter, *Europhys. Lett.* **139**, 67001 (2022).
- [23] M. J. Bowick, N. Fakhri, M. C. Marchetti, and S. Ramaswamy, Symmetry, thermodynamics, and topology in active matter, *Phys. Rev. X* **12**, 010501 (2022).
- [24] I. H. Riedel, K. Kruse, and J. Howard, A self-organized vortex array of hydrodynamically entrained sperm cells, *Science* **309**, 300 (2005).
- [25] E. Lauga, W. R. DiLuzio, G. M. Whitesides, and H. A. Stone, Swimming in circles: Motion of bacteria near solid boundaries, *Biophys. J.* **90**, 400 (2006).
- [26] A. P. Petroff, X. L. Wu, and A. Libchaber, Fast-moving bacteria self-organize into active two-dimensional crystals of rotating cells, *Phys. Rev. Lett.* **114**, 158102 (2015).
- [27] H. Li, H. Chaté, M. Sano, X.-q. Shi, and H. P. Zhang, Robust edge flows in swarming bacterial colonies, *Phys. Rev. X* **14**, 041006 (2024).
- [28] I. S. Aranson, Bacterial active matter, *Rep. Prog. Phys.* **85**, 076601 (2022).
- [29] K. Kim, N. Yoshinaga, S. Bhattacharyya, H. Nakazawa, M. Umetsu, and W. Teizer, Large-scale chirality in an active layer of microtubules and kinesin motor proteins, *Soft Matter* **14**, 3221 (2018).
- [30] Z. Dunajova, B. P. Mateu, P. Radler, K. Lim, D. Brandis, P. Velicky, J. G. Danzl, R. W. Wong, J. Elgeti, E. Hannezo, and M. Loose, Chiral and nematic phases of flexible active filaments, *Nat. Phys.* **19**, 1916 (2023).
- [31] F. Kümmel, B. Ten Hagen, R. Wittkowski, I. Buttinoni, R. Eichhorn, G. Volpe, H. Löwen, and C. Bechinger, Circular motion of asymmetric self-propelling particles, *Phys. Rev. Lett.* **110**, 198302 (2013).
- [32] B. A. Grzybowski, H. A. Stone, and G. M. Whitesides, Dynamic self-assembly of magnetized, millimetre-sized objects rotating at a liquid–air interface, *Nature (London)* **405**, 1033 (2000).
- [33] V. Soni, E. S. Bililign, S. Magkiriadou, S. Sacanna, D. Bartolo, M. J. Shelley, and W. T. M. Irvine, The odd free surface flows of a colloidal chiral fluid, *Nat. Phys.* **15**, 1188 (2019).
- [34] A. Bricard, J.-B. Caussin, N. Desreumaux, O. Dauchot, and D. Bartolo, Emergence of macroscopic directed motion in populations of motile colloids, *Nature (London)* **503**, 95 (2013).
- [35] J. Elgeti, R. G. Winkler, and G. Gompper, Physics of microswimmers-single particle motion and collective behavior: A review, *Rep. Prog. Phys.* **78**, 056601 (2015).
- [36] E. Lauga, Bacterial hydrodynamics, *Annu. Rev. Fluid Mech.* **48**, 105 (2016).
- [37] L. Lettermann, F. Ziebert, and U. S. Schwarz, A geometrical theory of gliding motility based on cell shape and surface flow, *Proc. Natl. Acad. Sci. USA* **121**, e2410708121 (2024).
- [38] C. L. Hueschen, L.-a. Segev-Zarko, J.-H. Chen, M. A. LeGros, C. A. Larabell, J. C. Boothroyd, R. Phillips, and A. R. Dunn, Emergent actin flows explain distinct modes of gliding motility, *Nat. Phys.* **20**, 1989 (2024).
- [39] L. Lettermann, F. Ziebert, M. Singer, F. Frischknecht, and U. S. Schwarz, Three-dimensional chiral active Ornstein-Uhlenbeck model for helical motion of microorganisms, *Phys. Rev. Lett.* **135**, 128403 (2025).
- [40] L. Lettermann, M. Singer, S. Steinbrück, F. Ziebert, S. Kanatani, P. Sinnis, F. Frischknecht, and U. S. Schwarz, Chirality of malaria parasites determines their motion patterns, *Nat. Phys.* **22**, 112 (2026).
- [41] A. Vilfan, L. Abbaspour, S. Villa, and V. Nasirimarekani, Chiral gliding: Right-handed navigation of filamentous cyanobacteria, *Proc. Natl. Acad. Sci. USA* **123**, e2534547123 (2026).
- [42] P. Patra, K. Beyer, A. Jaiswal, A. Battista, K. Rohr, F. Frischknecht, and U. S. Schwarz, Collective migration reveals mechanical flexibility of malaria parasites, *Nat. Phys.* **18**, 586 (2022).
- [43] M. G. Athani, N. Prouse, N. Sarpangala, P. Noerr, G. Schiano-Lomoriello, A. G. Kumar, F. L. Memarian, J. Gaillard, L. Blanchoin, L. S. Hirst, K. Dasbiswas, A. Gopinathan, O. Kučera, and D. A. Beller, Gliding microtubules exhibit

- tunable collective rotation driven by chiral active forces, [arXiv:2507.00245](#).
- [44] S. Chahal and B. Chakrabarti, Hydrodynamic instabilities in driven chiral suspensions, *Phys. Rev. E* **113**, L023101 (2026).
- [45] K. Copenhagen, R. Alert, N. S. Wingreen, and J. W. Shaevitz, Topological defects promote layer formation in *Myxococcus xanthus* colonies, *Nat. Phys.* **17**, 211 (2021).
- [46] E. Han, C. Fei, R. Alert, K. Copenhagen, M. D. Koch, N. S. Wingreen, and J. W. Shaevitz, Local polar order controls mechanical stress and triggers layer formation in *Myxococcus xanthus* colonies, *Nat. Commun.* **16**, 952 (2025).
- [47] M. C. Marchetti, J. F. Joanny, S. Ramaswamy, T. B. Liverpool, J. Prost, M. Rao, and R. A. Simha, Hydrodynamics of soft active matter, *Rev. Mod. Phys.* **85**, 1143 (2013).
- [48] M. Bär, R. Großmann, S. Heidenreich, and F. Peruani, Self-propelled rods: Insights and perspectives for active matter, *Annu. Rev. Condens. Matter Phys.* **11**, 441 (2020).
- [49] J. Herrou and T. Mignot, Dynamic polarity control by a tunable protein oscillator in bacteria, *Curr. Opin. Cell Biol.* **62**, 54 (2020).
- [50] Q. Vagne and G. Salbreux, Generic theory of interacting, spinning, active polar particles: A model for cell aggregates, *Phys. Rev. E* **111**, 014423 (2025).
- [51] P. Kraikivski, R. Lipowsky, and J. Kierfeld, Enhanced ordering of interacting filaments by molecular motors, *Phys. Rev. Lett.* **96**, 258103 (2006).
- [52] A. Baskaran and M. C. Marchetti, Enhanced diffusion and ordering of self-propelled rods, *Phys. Rev. Lett.* **101**, 268101 (2008).
- [53] S. Santhosh, M. R. Nejad, A. Doostmohammadi, J. M. Yeomans, and S. P. Thampi, Activity induced nematic order in isotropic liquid crystals, *J. Stat. Phys.* **180**, 699 (2020).
- [54] G. Liu, A. Patch, F. Bahar, D. Yllanes, R. D. Welch, M. C. Marchetti, S. Thutupalli, and J. W. Shaevitz, Self-driven phase transitions drive *Myxococcus xanthus* fruiting body formation, *Phys. Rev. Lett.* **122**, 248102 (2019).
- [55] S. Das, M. Ciarchi, Z. Zhou, J. Yan, J. Zhang, and R. Alert, Flocking by turning away, *Phys. Rev. X* **14**, 031008 (2024).
- [56] A. Maitra and M. Lenz, Spontaneous rotation can stabilise ordered chiral active fluids, *Nat. Commun.* **10**, 920 (2019).
- [57] A. Maitra, Activity unmasks chirality in liquid-crystalline matter, *Annu. Rev. Condens. Matter Phys.* **16**, 275 (2025).
- [58] M. E. Cates and J. Tailleur, Motility-induced phase separation, *Annu. Rev. Condens. Matter Phys.* **6**, 219 (2015).
- [59] T. Speck, Collective forces in scalar active matter, *Soft Matter* **16**, 2652 (2020).
- [60] J. Zhang, R. Alert, J. Yan, N. S. Wingreen, and S. Granick, Active phase separation by turning towards regions of higher density, *Nat. Phys.* **17**, 961 (2021).
- [61] S. Ramaswamy, R. A. Simha, and J. Toner, Active nematics on a substrate: Giant number fluctuations and long-time tails, *Europhys. Lett.* **62**, 196 (2003).
- [62] R. Großmann, I. S. Aranson, and F. Peruani, A particle-field approach bridges phase separation and collective motion in active matter, *Nat. Commun.* **11**, 5365 (2020).
- [63] S. Fürthauer, M. Strempel, S. W. Grill, and F. Jülicher, Active chiral fluids, *Eur. Phys. J. E* **35**, 89 (2012).
- [64] S. Fürthauer, M. Strempel, S. Grill, and F. Jülicher, Active chiral processes in thin films, *Phys. Rev. Lett.* **110**, 048103 (2013).
- [65] F. Jülicher, S. W. Grill, and G. Salbreux, Hydrodynamic theory of active matter, *Rep. Prog. Phys.* **81**, 076601 (2018).
- [66] B. Sabass, M. D. Koch, G. Liu, H. A. Stone, and J. W. Shaevitz, Force generation by groups of migrating bacteria, *Proc. Natl. Acad. Sci. USA* **114**, 7266 (2017).
- [67] L. A. Hoffmann, K. Schakenraad, R. M. H. Merks, and L. Giomi, Chiral stresses in nematic cell monolayers, *Soft Matter* **16**, 764 (2020).
- [68] V. Yashunsky, D. J. G. Pearce, C. Blanch-Mercader, F. Ascione, P. Silberzan, and L. Giomi, Chiral edge current in nematic cell monolayers, *Phys. Rev. X* **12**, 041017 (2022).
- [69] A. Barbot, D. Decanini, and G. Hwang, Controllable roll-to-swim motion transition of helical nanoswimmers, *IEEE Int. Conf. Intell. Robot. Syst.* 4662 (2014).
- [70] X. Liang, Y. Ding, Z. Yuan, Y. Han, Y. Zhou, J. Jiang, Z. Xie, P. Fei, Y. Sun, P. Jia, G. Gu, Z. Zhong, F. Chen, G. Si, and Z. Gong, Mechanics of soft-body rolling motion without external torque, *Phys. Rev. Lett.* **134**, 198401 (2025).
- [71] A. Be'er, E. D. Neimand, D. Corbett, D. J. G. Pearce, G. Ariel, and V. Yashunsky, Irreversibility and symmetry breaking in the creation and annihilation of defects in active living matter, [arXiv:2508.15622](#).
- [72] S. Thutupalli, M. Sun, F. Bunyak, K. Palaniappan, and J. W. Shaevitz, Directional reversals enable *Myxococcus xanthus* cells to produce collective one-dimensional streams during fruiting-body formation, *J. R. Soc. Interface* **12**, 20150049 (2015).
- [73] C. Dinet, A. Michelot, J. Herrou, and T. Mignot, Linking single-cell decisions to collective behaviours in social bacteria, *Phil. Trans. R. Soc. B* **376**, 20190755 (2021).
- [74] A. Shrivastava, V. K. Patel, Y. Tang, S. C. Yost, F. E. Dewhirst, and H. C. Berg, Cargo transport shapes the spatial organization of a microbial community, *Proc. Natl. Acad. Sci. USA* **115**, 8633 (2018).
- [75] D. Nakane, S. Odaka, K. Suzuki, and T. Nishizaka, Large-scale vortices with dynamic rotation emerged from monolayer collective motion of gliding *Flavobacteria*, *J. Bacteriol.* **203**, e00073 (2021).