

Pseudogiant Number Fluctuations and Nematic Order in Microswimmer Suspensions

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(Received 29 March 2025; revised 23 June 2025; accepted 6 August 2025; published 27 August 2025)

Giant number fluctuations (GNFs), whereby the standard deviation ΔN in the local number of particles $\langle N \rangle$ grows faster than $\sqrt{\langle N \rangle}$, are a hallmark property of dry active matter systems with orientational order, such as a collection of granular particles on a vibrated plate. This contrasts with momentum-conserving (“wet”) active matter systems, such as suspensions of swimming bacteria, where no theoretical prediction of GNFs exist, although numerous experimental observations of such enhanced fluctuations have been reported. In this Letter, we numerically confirm the emergence of super-Gaussian number fluctuations in a three-dimensional suspension of pusher microswimmers undergoing a transition to collective motion. These fluctuations emerge sharply above the transition, but only for sufficiently large values of the bacterial persistence length $\ell_p = v_s/\lambda$, where v_s is the bacterial swimming speed and λ the tumbling rate. Crucially, these “pseudo-GNFs” differ from true GNFs, as they only occur on length scales shorter than the typical size ξ of nematic patches in the collective motion state, which is in turn proportional to the single-swimmer persistence length ℓ_p . Our results thus suggest that observations of enhanced density fluctuations in biological active matter systems actually represent transient effects that decay away beyond mesoscopic length scales and raises the question to what extent “true” GNFs with universal properties can exist in the presence of fluid flows.

DOI: [10.1103/31q1-hj3n](https://doi.org/10.1103/31q1-hj3n)

Collective motion in active matter typically arises due to the coupling between activity and orientational order [1]. One generic feature of orientationally ordered flocks is the emergence of anomalously large fluctuations in the particle density, so-called giant number fluctuations (GNFs), whereby the standard deviation ΔN in the local number of particles N grows as $\langle N \rangle^\alpha$ with $\alpha > 1/2$ [2]. Experimentally, the emergence of GNFs in dry active matter was first demonstrated in a collection of rods on a vibrating plate [3], where collective motion arises from the coupling between activity-driven particle currents and (quasi)long-range order caused by particle collisions, and has since then been experimentally [4,5] and numerically [6,7] verified in both nematic and polar flocks. The emergence of GNFs in dry flocks can be understood by calculating the autocorrelation of density fluctuations in the

orientationally ordered state [8,9]. In the nematic case, the ensuing analysis shows that, at linear level, the variance $\langle \delta n(\mathbf{q}, t) \delta n(-\mathbf{q}, t) \rangle$ in the local number density n of the ordered flock diverges as q^{-2} for small $q = |\mathbf{q}|$, which, in two dimensions, yields a linear growth of ΔN with $\langle N \rangle$, i.e., $\alpha = 1$. This picture is changed when accounting for the effect of nonlinearities [10], which lead to nonuniversal exponents that depend on the microscopic model parameters.

In wet active matter, the situation is more complex: Since the nematically ordered state is generically unstable for finite wave numbers in the presence of fluid flows [11], the route used in the dry case to calculate $\langle \delta n(\mathbf{q}, t) \delta n(-\mathbf{q}, t) \rangle$, based on a computation at linear level followed by the treatment of nonlinearities within a renormalization group framework [8,10], is no longer accessible. Therefore, no quantitative predictions exist for the emergence of GNFs in bulk wet active nematics, although they have been predicted for nematic flocks moving through a fluid in contact with a substrate [12]. There are, however, numerous experimental [13–17] (and some numerical [18]) observations of enhanced concentration fluctuations in various biological incarnations of wet active matter, suggesting that

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such fluctuations are indeed a common feature also in the presence of momentum conservation; it is, however, difficult to assess whether these observations represent true GNFs with asymptotically valid power laws and associated universal exponents or merely transient effects where fluctuations appear non-Gaussian because distributional convergence has not yet been reached.

The archetypical example of collective motion in wet active matter is the transition to so-called bacterial turbulence in dilute suspensions of rear-actuated “pusher” microorganisms such as *Escherichia coli* and *Bacillus subtilis* [19–22]. In a three-dimensional, unbounded suspension of pusher microswimmers at density n , this transition is predicted to occur whenever [23–25]

$$n > n_c^\infty = \frac{5\lambda}{\kappa}, \quad (1)$$

where $\kappa > 0$ is the dipole strength and λ is the rate of bacterial reorientation (“tumbles”). The critical density in Eq. (1) represents the long-wavelength destabilization of the homogeneous and isotropic suspension caused by bacterial reorientation due to flow alignment. Since the dipolar flow field is fore-aft symmetric, the ensuing orientationally ordered state exhibits nematic symmetry. This state, however, in turn destabilizes due to the presence of fluid flows [11], resulting in a highly nonlinear, turbulent state characterized by short-ranged nematic order and long-range chaotic flows [26,27]. The fore-aft symmetry is broken by the presence of self-propulsion, whereby each swimmer moves along its director $\mathbf{p}$ with constant speed v_s . Crucially, however, v_s does *not* affect the mean-field critical density in Eq. (1) [28]; this observation is far from trivial, as exemplified by the emergence of collective motion near a confining boundary, where v_s enters the expression for n_c even at mean-field level [29,30].

In this Letter, we numerically confirm the experimental observation that super-Gaussian number fluctuations occur generically above the transition to collective motion in microswimmer suspensions. Unlike in dry active systems, however, these only occur on length scales small compared to the bacterial persistence length $\ell_p = v_s/\lambda$, beyond which number fluctuations start decaying toward Gaussian behavior. By analyzing the range of orientational order in the collective motion regime, we show that the linear size ξ of nematically ordered patches is also proportional (and comparable) to ℓ_p , establishing a direct link between nematic order and non-Gaussian number fluctuations. Our results demonstrate that true GNFs, in the sense of being a large-scale property exhibiting universal exponents, are generically suppressed in the presence of fluid flow, providing a new perspective on experimental observations of anomalous number fluctuations in wet active systems [13–17].

We consider a dilute, three-dimensional suspension of pusher microswimmers at nominal number density n moving through an incompressible, viscous fluid with viscosity μ and mass density ρ . Each swimmer is modeled as an extended force dipole of magnitude $\kappa = F\ell/\mu$ acting on the fluid, with F the force magnitude and ℓ the dipole length. The position $\mathbf{r}_i$ and orientation $\mathbf{p}_i$ of swimmer i evolve according to

$$\dot{\mathbf{r}}_i = v_s \mathbf{p}_i + \mathbf{U}(\mathbf{r}_i), \quad (2)$$

$$\dot{\mathbf{p}}_i = (\mathbb{I} - \mathbf{p}_i \mathbf{p}_i) \cdot \nabla \mathbf{U}(\mathbf{r}_i) \cdot \mathbf{p}_i, \quad (3)$$

where $\mathbf{U}(\mathbf{r}_i)$ is fluid velocity measured at the position of the swimmer body, v_s is the (constant) swimming speed, and $\mathbb{I}$ is the unit tensor. In addition to the rotation by the ambient fluid described by Eq. (3), each swimmer randomizes its swimming direction (tumbles) with average frequency λ . The temporal evolution of the flow field $\mathbf{U}(\mathbf{r}, t)$ was solved using a point-force implementation of the lattice Boltzmann (LB) algorithm described previously [25,26,31,32], using a cubic box of linear size H with periodic boundaries; parameter values and technical details about the simulations are provided as End Matter.

We begin by characterizing the transition from disordered swimming to collective motion and, in particular, the effect of varying swimming speed v_s . As an order parameter, we choose the reduced space- and time-averaged fluid velocity variance, $\langle U^2 \rangle / \langle U^2 \rangle_0$, where $\langle U^2 \rangle_0$ is the corresponding value measured in suspension of noninteracting microswimmers. In Fig. 1, we plot this quantity as a function of the reduced microswimmer density $n/n_c(H)$, where $n_c(H)$ is the analytically known critical density in a finite system of linear size H [33],

$$n_c(H) = n_c^\infty \left[1 + \frac{3\pi \ell_p}{5H} + \frac{4\pi^2}{5} \left(\frac{\ell_p}{H} \right)^2 \right]. \quad (4)$$

Equation (4) encodes the fact that the mean-field hydrodynamic instability leading to bacterial turbulence occurs at the longest length scale available, which, in a system of linear size H , corresponds to a critical wave vector $k_c = 2\pi/H$. Using this correction, the results in Fig. 1 confirm the theoretical prediction from [28] that faster swimming effectively sharpens the transition to collective motion by suppressing pretransitional swimmer-swimmer correlations without shifting the critical density. This sharpening is therefore *not* a finite-size effect: As we show in Supplemental Material [34] (see also Refs. [25,26]), increasing H does not lead to a sharpening of the transition, unlike what one would expect from a critical phase transition. The analysis in Fig. 1 also shows that the theoretically predicted critical density given by Eqs. (1) and (4) coincides with the sharp increase in $\langle U^2 \rangle$. Even though the transition to collective motion has been

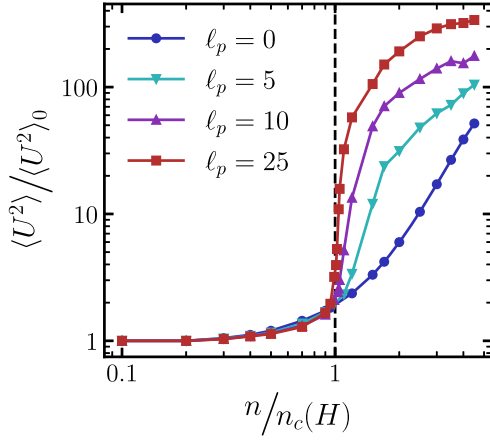


FIG. 1. Fluid velocity variance $\langle U^2 \rangle$ normalized by its corresponding value in a noninteracting suspension $\langle U^2 \rangle_0$ for various persistence lengths ℓ_p . The microswimmer density n is normalized by the critical density $n_c(H)$ from Eqs. (1) and (4). Note that increasing the swimming speed, as measured through ℓ_p , sharpens the transition by suppressing pretransitional swimmer-swimmer correlations.

numerically studied numerous times using continuum [27] and particle-resolved [18,26] simulations, the results in Fig. 1 constitute the first quantitative verification of the prediction in Eq. (1). As seen in the snapshots in End Matter, changing ℓ_p leads to visible differences in the collective steady states: For $\ell_p = 0$, the flow field appears random with very short-ranged correlations even for $n/n_c = 2$, while faster swimming, corresponding to larger ℓ_p , leads to increasingly large-scale flow structures in the velocity field.

To quantify the emergence of non-Gaussian number fluctuations at the transition to collective motion, we first consider the spatiotemporal average $\langle N \rangle$ and the corresponding standard deviation ΔN of the number of particles in randomly sampled spherical volumes of varying radius R . For $n > n_c$ and $\ell_p > 0$, it is clear from the results in Fig. 2(a) that ΔN grows faster than $\sqrt{\langle N \rangle}$, indicating the emergence of GNFs in the collective motion state. For shakers ($\ell_p = v_s = 0$), no such enhanced fluctuations are seen, which, as was first noted in [35], is a consequence of the fact that the local polar order which drives density fluctuations is strictly zero for shakers, since there is no term in the microscopic equations of motion that break fore-aft symmetry. For finite ℓ_p , $\Delta N/\sqrt{\langle N \rangle}$ has a non-monotonic behavior, with significantly enhanced number fluctuations for small and intermediate $\langle N \rangle$, followed by a fast decrease for larger $\langle N \rangle$. This behavior is qualitatively similar to previous experimental [3–5,13,15–17] and numerical [6,7] observations of GNFs and can partially be explained by the unavoidable damping of number fluctuations at large length scales due to global particle

conservation; as we will see in the following, this is, however, not the primary mechanism at work here. That the underlying physics is more complex than just mass conservation is already visible from the two curves for $\ell_p = 5$ in Figs. 2(a) and 2(b): These show that increasing the system size from $H = 100$ to $H = 250$ does *not* extend the region of enhanced number fluctuations as expected for true GNFs, but rather leads to the development of an intermediate plateau with Gaussian fluctuations preceding the decay due to finite H .

Because of the difficulty in consistently fitting a power law to the very limited data range, in Fig. 2(b) we instead approximate the derivative $d \log \Delta N / d \log \langle N \rangle$ by differentiating a high-order polynomial fitted to the data in Fig. 2(a). From these data, we operationally define the *apparent* GNF exponent α_{app} as the maximum in $d \log \Delta N / d \log \langle N \rangle$, located at $R \equiv R^*$, as shown in Fig. 2(b). Based on this analysis, in Fig. 2(c) we plot α_{app} as a function of n , demonstrating the sharp onset of non-Gaussian concentration fluctuations at $n = n_c$. Even given the limitations of its operational definition, it is clear that α_{app} does not approach any universal value, as it depends strongly on both ℓ_p and on n , with a maximum slightly above n_c . Unsurprisingly, α_{app} also exhibits strong finite-size effects, although it asymptotes to a characteristic value for each ℓ_p as H becomes sufficiently large [34].

To investigate the origin of the nonmonotonic behavior in Fig. 2(a), in Fig. 2(d) we plot R^* , which characterizes the length scale at which density fluctuations are maximized, as a function of the system size H . For true GNFs, one expects the region where non-Gaussian fluctuations are observed to grow in an unbounded fashion with H , approaching a universal power law in the thermodynamic limit. Here, R^* instead exhibits an initial increase until it saturates at $R^* \approx 0.8\ell_p$ for $H \approx 20\ell_p$. (The suboptimal data collapse for $\ell_p = 15$ is an inertial effect, which we discuss further below.) This analysis clearly shows that the non-Gaussian fluctuations that emerge above n_c are not true GNFs in the sense of being a universal property that survives in the thermodynamic limit, but rather “pseudo-GNFs” that occur transiently over mesoscopic length scales. These results establish that R^* is directly proportional to ℓ_p above the transition to collective motion, although their relationship contains a density-dependent prefactor that we expect to remain close to unity reasonably far above n_c .

In dry active systems, GNFs arise due to the coupling between (quasi)long-range orientational order and non-equilibrium dynamics [2,8]. In the presence of a fluid, the emergent, orientationally ordered state described by the instability criterion of Eq. (1) is, however, unstable for finite wave numbers [11], resulting in the chaotic motion that is characteristic of the turbulent state. To establish a connection between local nematic order and the pseudo-GNFs established in Fig. 2, we calculate the distance-dependent, scalar swimmer-swimmer nematic order

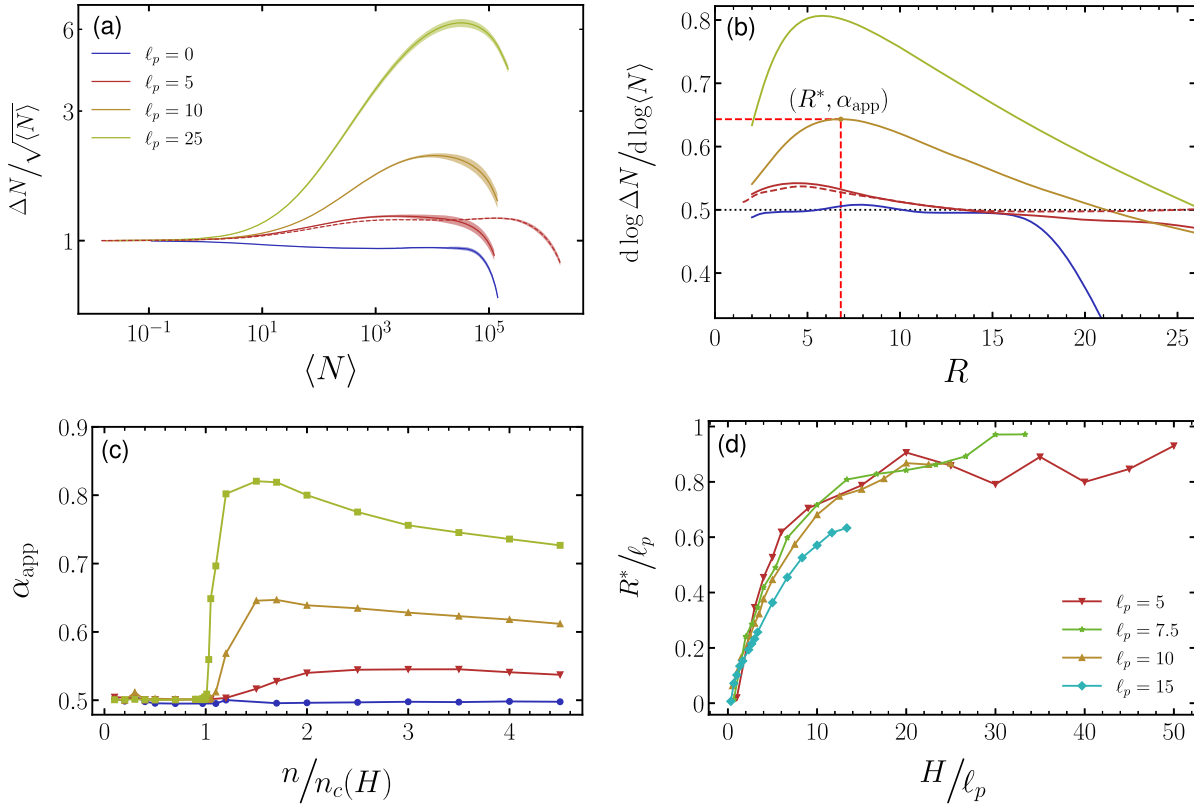


FIG. 2. (a) Reduced standard deviation $\Delta N / \sqrt{\langle N \rangle}$ of the average number of particles N in a spherical volume as a function of $\langle N \rangle$ obtained for $n/n_c = 2.0$ and various ℓ_p , as indicated. The dashed line for $\ell_p = 5$ shows the same quantity for a larger system size, $H = 250$, showing the development of an extended plateau of Gaussian fluctuations for intermediate length scales. The shaded area denotes one standard deviation, estimated by averaging each run over ten subbatches. (b) The derivative $d \log \Delta N / d \log \langle N \rangle$ plotted as a function of the radius R of the sampling volume. The maximum in $d \log \Delta N / d \log \langle N \rangle$ defines the apparent GNF exponent α_{app} , and its location defines R^* . (c) α_{app} as a function of the reduced microswimmer density n/n_c . Notice that non-Gaussian fluctuations emerge at the transition to collective motion only for sufficiently large ℓ_p and are completely absent for shakers. (d) R^* / ℓ_p as a function of the reduced system size H / ℓ_p for $n/n_c = 2.0$. The data collapse shows that, for sufficiently large system sizes $H \gg \ell_p$, R^* is controlled by ℓ_p ; hence, the apparently non-Gaussian fluctuations are only transient.

$S(r) \equiv \frac{1}{2} \langle 3 \cos^2 \theta - 1 \rangle_r$, where θ is the angle formed between the two swimmer orientation vectors and $\langle \cdots \rangle_r$ denotes a spatiotemporal average over all swimmer pairs with a given separation r . For $\ell_p = 0$, we find that $S(r)$ is well fitted by a stretched exponential, $S(r) = S_0 e^{-(r/\xi)^\beta}$ with a single decay length ξ and a weakly density-dependent β ranging between 1.05 and 1.5 [34]. For $\ell_p > 0$, $S(r)$ has a complex shape with no obvious analytical description [26], and we therefore instead fit the initial decay of $S(r)$ using a regular exponential form, $S(r) = S_0 e^{-r/\xi}$ [34]. In spite of this complexity, for both shakers and swimmers it is natural to interpret ξ as the characteristic linear size of nematic patches in the turbulent state. In Fig. 3(a) we show the extracted values of ξ as a function of n/n_c for the same parameter set as in Fig. 2(c). Even though the jump in ξ at $n = n_c$ is less sharp than for α_{app} , the similarity between the two datasets is striking, and it is clear that the onset of collective motion for large ℓ_p is

characterized by a sharp increase in the range of nematic order. In Fig. 3(b), we further plot ξ as a function of ℓ_p for $n/n_c = 2.0$ and four different H . Even though finite-size effects are large, the four datasets all present the same linear scaling of ξ on ℓ_p , although the large- ℓ_p behavior is likely also affected by swimmer inertia, as discussed below. This result strongly suggests that the size of nematic patches in an unbounded system at a given $n/n_c > 1$ is directly controlled by ℓ_p . This finding might initially seem surprising, since the most unstable wave number of the homogeneous and isotropic state encoded in Eq. (4) corresponds to the largest available length scale in the system [29]. However, ξ is more likely controlled by the (finite) smallest stable wave number of the nematic state, which we expect to set the maximum size of stable nematic patches in the turbulent state, similar to what has been found previously for continuum active nematics [36]. In End Matter, we show how, starting from a mean-field description of the

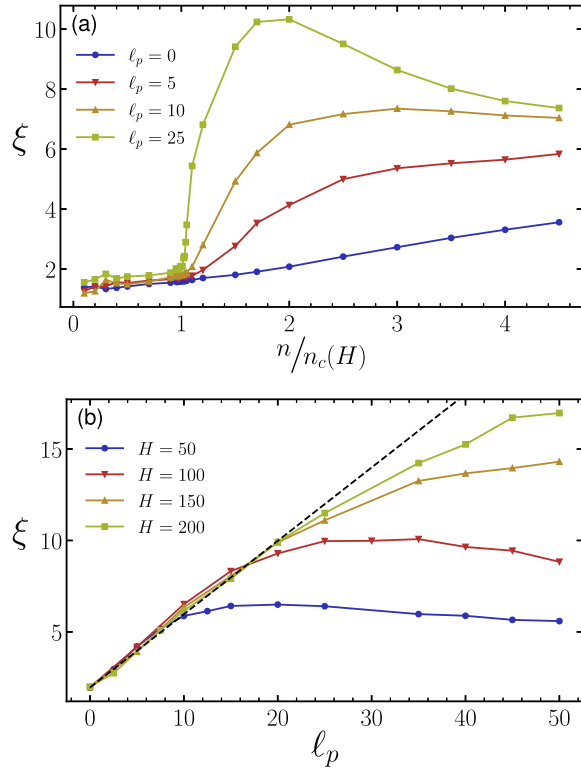


FIG. 3. (a) Fitted values of the nematic length scale ξ as a function of the reduced microswimmer density for $H = 100$ and various ℓ_p , as indicated. Notice the similarity with the data in Fig. 2(c). (b) ξ plotted as a function of ℓ_p for $n/n_c = 2.0$ and four different values of H , as indicated. The dashed line shows a linear fit to the first six data points for $H = 200$.

microswimmer suspension in terms of the relevant mesoscopic order parameter fields [35,37,38], the persistence length ℓ_p and tumbling time λ^{-1} emerge as the natural length and timescales for nondimensionalizing the resulting equations. When rescaled in this manner, these equations depend on a single dimensionless control parameter, namely, n/n_c . By this argument, *any* length scale $\tilde{\ell}^*$ emerging as a result of interactions between microswimmers can be written in dimensionless form as $\tilde{\ell}^* = f(n/n_c)$, where f is an unknown function, so that the corresponding dimensional length scale becomes $\ell^* = \ell_p f(n/n_c)$. This implies that ℓ_p sets the scale for *all* emergent properties of the collective motion state, including the linear size of nematic patches as measured through ξ in Fig. 3(b).

The results presented in this Letter thus establish a clear connection between (i) the characteristic length scale over which non-Gaussian concentration fluctuations are observed, as encoded in R^* , and (ii) the linear size of nematic patches in the turbulent regime, as encoded in ξ . We observe that number fluctuations inside a nematic patch grow until reaching $R^* \approx \xi$, where the latter length scale is selected by the largest stable length scale of a nematic

ordered state in the presence of fluid flows [8]. At scales much larger than ξ , the orientational correlations between individual patches vanish [26], restoring Gaussian fluctuations as in equilibrium. Thus, the non-Gaussian number fluctuations observed in our model do not constitute an example of GNFs in the universal sense, which is a direct consequence of the absence of a stable, nematically ordered state. Since this instability is generic in the presence of fluid flows and occurs for arbitrary values of activity, whether extensile or contractile [11], our results suggest that true GNFs are in fact generically absent from nematically aligning, momentum-conserving active systems. Most importantly, this conclusion includes wet active nematics [39], for which most previous studies of active turbulence have been conducted. The primary difference between this class of continuum models and the microswimmer suspensions studied here is the origin of the initial instability of the isotropic state. In microswimmers, this stems from the flow alignment equation (3), while for an active nematic it is typically (although not exclusively [40]) caused by an underlying free energy that induces an isotropic-nematic transition even in the absence of activity. However, since the ensuing collective motion state is fundamentally caused by the same instability [11] in both models, our conclusions about the absence of true GNFs holds equally for both classes of systems.

Our results show that both ξ and R^* are directly proportional to the microscopic persistence length ℓ_p , showing that, even though v_s is absent from the instability criterion in Eq. (1), swimming has a profound effect on the properties of both the pretransitional suspension [28] and the turbulent state. Since $R^* \sim \xi \sim \ell_p$, there exists a possibility of restoring universal GNFs in the limit $\ell_p \rightarrow \infty$: Because α_{app} is strictly bounded by unity, the results in Fig. 2 suggest that, for sufficiently large ℓ_p and $H \gg \ell_p$, one might recover an extended power-law region with a universal exponent. Extending the numerics to larger ℓ_p is, however, computationally prohibitive, for two reasons: First of all, reaching $H \gg \ell_p$ requires massive system sizes, which limits the data range in Fig. 2(d). Second, since the LB method intrinsically operates at finite Reynolds number, increasing v_s eventually leads to non-negligible effects of swimmer inertia, which become significant for $\text{Re} \equiv v_s \ell_p \rho / \mu \geq 0.1$ [31,41]. For the current parameter set, this translates to $\ell_p \geq 9$, in agreement with the observed decline in the data collapse in Fig. 2(d). An alternative approach is a field-theoretical treatment of the emergence of non-Gaussian fluctuations, similar to the strategy used in the dry case [8–10]. A direct translation of this approach to wet systems is, however, not possible even at linear level, as it relies on the long-wavelength perturbation of a stable, nematically ordered base state, which is absent in the presence of fluid flows.

Regardless of whether or not true GNFs are formally restored in the $\ell_p \rightarrow \infty$ limit, our data clearly establish that

GNFs in the universal sense cannot be generically expected in wet active systems with underlying nematic order. Our results thus provide a new perspective on observations of non-Gaussian fluctuations in biological realizations of active matter [13–17] as well as novel insights into the factors that control the emergent properties of collective motion in bacterial suspensions.

Acknowledgments—Helpful discussions with Sriram Ramaswamy, Ananyo Maitra, and Eric Clément are kindly acknowledged. J. S. acknowledges funding from the Knut and Alice Wallenberg Foundation (Grant No. 2019.0079) and the Swedish Research Council (Grant No. 2019-03718).

Data availability—The data that support the findings of this Letter are not publicly available upon publication because it is not technically feasible and/or the cost of preparing, depositing, and hosting the data would be prohibitive within the terms of this research project. The data are available from the authors upon reasonable request.

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- [1] 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).
 - [2] S. Ramaswamy, The mechanics and statistics of active matter, *Annu. Rev. Fluid Mech.* **1**, 323 (2010).
 - [3] V. Narayan, S. Ramaswamy, and N. Menon, Long-lived giant number fluctuations in a swarming granular nematic, *Science* **317**, 105 (2007).
 - [4] N. Kumar, H. Soni, S. Ramaswamy, and A. K. Sood, Flocking at a distance in active granular matter, *Nat. Commun.* **5**, 4688 (2014).
 - [5] J. Deseigne, O. Dauchot, and H. Chaté, Collective motion of vibrated polar disks, *Phys. Rev. Lett.* **105**, 098001 (2010).
 - [6] H. Chaté, F. Ginelli, and R. Montagne, Simple model for active nematics: Quasi-long-range order and giant fluctuations, *Phys. Rev. Lett.* **96**, 180602 (2006).
 - [7] H. Chaté, F. Ginelli, G. Grégoire, and F. Raynaud, Collective motion of self-propelled particles interacting without cohesion, *Phys. Rev. E* **77**, 046113 (2008).
 - [8] 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).
 - [9] J. Toner, Giant number fluctuations in dry active polar fluids: A shocking analogy with lightning rods, *J. Chem. Phys.* **150**, 154120 (2019).
 - [10] S. Shankar, S. Ramaswamy, and M. C. Marchetti, Low-noise phase of a two-dimensional active nematic system, *Phys. Rev. E* **97**, 012707 (2018).
 - [11] R. A. Simha and S. Ramaswamy, Hydrodynamic fluctuations and instabilities in ordered suspensions of self-propelled particles, *Phys. Rev. Lett.* **89**, 058101 (2002).
 - [12] A. Maitra, P. Srivastava, M. C. Marchetti, J. S. Lintuvuori, S. Ramaswamy, and M. Lenz, A nonequilibrium force can stabilize 2D active nematics, *Proc. Natl. Acad. Sci. U.S.A.* **115**, 6934 (2018).
 - [13] Z. Liu, W. Zeng, X. Ma, and X. Cheng, Density fluctuations and energy spectra of 3D bacterial suspensions, *Soft Matter* **17**, 10806 (2021).
 - [14] G. Duclos, S. Garcia, H. G. Yevick, and P. Silberzan, Perfect nematic order in confined monolayers of spindle-shaped cells, *Soft Matter* **10**, 2346 (2014).
 - [15] D. Nishiguchi, K. H. Nagai, H. Chaté, and M. Sano, Long-range nematic order and anomalous fluctuations in suspensions of swimming filamentous bacteria, *Phys. Rev. E* **95**, 020601(R) (2017).
 - [16] F. Peruani, J. Starruß, V. Jakovljevic, L. Søgaaard-Andersen, A. Deutsch, and M. Bär, Collective motion and nonequilibrium cluster formation in colonies of gliding bacteria, *Phys. Rev. Lett.* **108**, 098102 (2012).
 - [17] H. P. Zhang, A. Be'er, E.-L. Florin, and H. L. Swinney, Collective motion and density fluctuations in bacterial colonies, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 13626 (2010).
 - [18] D. Saintillan and M. J. Shelley, Emergence of coherent structures and large-scale flows in motile suspensions, *J. R. Soc. Interface* **9**, 571 (2012).
 - [19] J. Gachelin, A. Rousselet, A. Lindner, and E. Clément, Collective motion in an active suspension of *Escherichia coli* bacteria, *New J. Phys.* **16**, 025003 (2014).
 - [20] A. Sokolov and I. S. Aranson, Physical properties of collective motion in suspensions of bacteria, *Phys. Rev. Lett.* **109**, 248109 (2012).
 - [21] J. Dunkel, S. Heidenreich, K. Dreschner, H. H. Wensink, M. Bär, and R. E. Goldstein, Fluid dynamics of bacterial turbulence, *Phys. Rev. Lett.* **110**, 228102 (2013).
 - [22] H. H. Wensink, J. Dunkel, S. Heidenreich, K. Drescher, R. E. Goldstein, H. Löwen, and J. M. Yeomans, Meso-scale turbulence in living fluids, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 14308 (2012).
 - [23] C. Hohenegger and M. J. Shelley, Stability of active suspensions, *Phys. Rev. E* **81**, 046311 (2010).
 - [24] G. Subramanian and D. L. Koch, Critical bacterial concentration for the onset of collective swimming, *J. Fluid Mech.* **632**, 359 (2009).
 - [25] J. Stenhammar, C. Nardini, R. W. Nash, D. Marenduzzo, and A. Morozov, Role of correlations in the collective behavior of microswimmer suspensions, *Phys. Rev. Lett.* **119**, 028005 (2017).
 - [26] D. Bárdfalvy, H. Nordanger, C. Nardini, A. Morozov, and J. Stenhammar, Particle-resolved lattice Boltzmann simulations of 3-dimensional active turbulence, *Soft Matter* **15**, 7747 (2019).
 - [27] D. Saintillan and M. J. Shelley, Instabilities, pattern formation, and mixing in active suspensions, *Phys. Fluids* **20**, 123304 (2008).
 - [28] V. Škultéty, C. Nardini, J. Stenhammar, D. Marenduzzo, and A. Morozov, Swimming suppresses correlations in dilute suspensions of pusher microorganisms, *Phys. Rev. X* **10**, 031059 (2020).
 - [29] V. Škultéty, D. Bárdfalvy, J. Stenhammar, C. Nardini, and A. Morozov, Hydrodynamic instabilities in a two-dimensional sheet of microswimmers embedded in a three-dimensional fluid, *J. Fluid Mech.* **980**, A28 (2024).

- [30] D. Bárdfalvy, V. Škultéty, C. Nardini, A. Morozov, and J. Stenhammar, Collective motion in a sheet of microswimmers, *Commun. Phys.* **7**, 93 (2024).
- [31] R. W. Nash, R. Adhikari, and M. E. Cates, Singular forces and pointlike colloids in lattice Boltzmann hydrodynamics, *Phys. Rev. E* **77**, 026709 (2008).
- [32] R. W. Nash, R. Adhikari, J. Tailleur, and M. E. Cates, Run-and-tumble particles with hydrodynamics: Sedimentation, trapping, and upstream swimming, *Phys. Rev. Lett.* **104**, 258101 (2010).
- [33] V. A. Martinez, E. Clément, J. Arlt, C. Douarche, A. Dawson, J. Schwarz-Linek, A. K. Creppy, V. Škultéty, A. N. Morozov, H. Auradou, and W. C. K. Poon, A combined rheometry and imaging study of viscosity reduction in bacterial suspensions, *Proc. Natl. Acad. Sci. U.S.A.* **117**, 2326 (2020).
- [34] See Supplemental Material containing finite-size scalings of fluid velocity variance and GNF exponents as well as fits used to extract the correlation lengths in Fig. 3, at <http://link.aps.org/supplemental/10.1103/31q1-hj3n> for further details.
- [35] D. Saintillan and M. J. Shelley, Theory of active suspensions, in *Complex Fluids in Biological Systems: Experiment, Theory, and Computation*, edited by S. E. Spagnolie (Springer, New York, 2015), pp. 319–355.
- [36] B. Martínez-Prat, J. Ignés-Mullol, J. Casademunt, and F. Sagués, Selection mechanism at the onset of active turbulence, *Nat. Phys.* **15**, 362 (2019).
- [37] V. Škultéty, Collective motion in microswimmer suspensions, Ph. D. thesis, The University of Edinburgh, 2023.
- [38] A. Baskaran and M. C. Marchetti, Statistical mechanics and hydrodynamics of bacterial suspensions, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 15567 (2009).
- [39] A. Doostmohammadi, J. Ignés-Mullol, J. Yeomans, and F. Sagués, Active nematics, *Nat. Commun.* **9**, 3246 (2018).
- [40] 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).
- [41] J. de Graaf and J. Stenhammar, Lattice-Boltzmann simulations of microswimmer-tracer interactions, *Phys. Rev. E* **95**, 023302 (2017).
- [42] K. Drescher, J. Dunkel, L. H. Cisneros, S. Ganguly, and R. E. Goldstein, Fluid dynamics and noise in bacterial cell-cell and cell-surface scattering, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 10940 (2011).

End Matter

Simulation details—In terms of LB units, defined by the lattice spacing ΔL and the time step Δt , the swimmer parameters were set to $F = 1.57 \times 10^{-3}$ and $\ell = 1$, roughly corresponding to the value of κ measured for *E. coli* [26,42], and $\lambda = 2 \times 10^{-4}$. We furthermore set $\mu = 1/6$, corresponding to full relaxation of the fluid to local equilibrium at each time step, and $\rho = 1$. As we showed in [28], a bulk microswimmer suspension is described by two control parameters: the reduced microswimmer density n/n_c^∞ , where n_c^∞ is given by Eq. (1), and the swimming persistence length $\ell_p = v_s/\lambda$. In order to keep n_c^∞ constant, ℓ_p was controlled by varying the swimming speed v_s between zero and 5×10^{-3} while keeping λ constant. All simulations were initialized from a configuration with random swimmer positions and orientations. All the data acquired before reaching steady state, as monitored through the time dependence of the fluid velocity variance $\langle U^2 \rangle$, were discarded from the analysis. Unless otherwise stated, results are presented for a system size $H = 100$ and all lengths are expressed in terms of the swimmer length ℓ .

ℓ_p dependence of collective flow fields—Figure 4 shows simulation snapshots of the flow field $\mathbf{U}$ deep in the collective motion state. These clearly show the strong effect of changing ℓ_p on the appearance and spatial correlations of the collective flow fields, which is also reflected in the increased range of nematic swimmer-swimmer correlations, as discussed in the main text.

Mean-field description of the suspension dynamics—Our starting point is a mean-field kinetic theory similar to those developed previously in the literature to describe dilute suspensions of dipolar, needlelike microswimmers [27,35,38]. While differing in technical details, all these theories encode the following simple microscopic dynamics: Each particle swims in the direction of its orientation with the swimming speed v_s , while randomly changing its orientation (tumbling) with

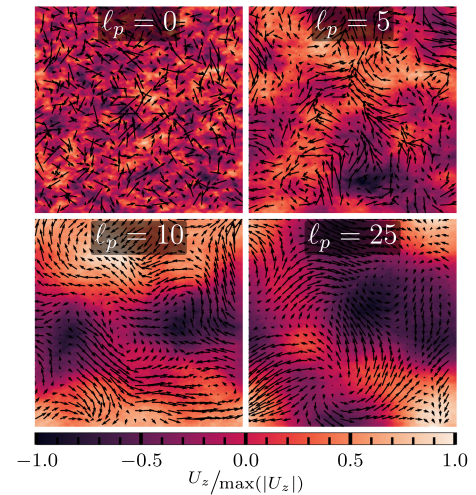


FIG. 4. Snapshots of a 2D slice of the 3D flow field for $n/n_c = 2.0$ and $H = 250$, for the values of ℓ_p indicated. Arrows show the in-plane component and colors show the out-of-plane component of $\mathbf{U}$, scaled by its maximum value.

a rate λ . Additionally, each microswimmer generates a long-ranged dipolar velocity field that advects and reorients all other microswimmers. The resulting kinetic theory allows one to identify the microswimmer density $c(\mathbf{r}, t)$, their average polarization $\mathbf{m}(\mathbf{r}, t)$, and the nematic order parameter $\mathbf{Q}(\mathbf{r}, t)$ as the crucial degrees of freedom to describe the transition to collective motion in such systems. Employing the same methods previously utilized in this context [35,38], we expand the one-particle distribution function of the kinetic theory in terms of its orientational moments (see Ref. [37] for details). Enslaving the third-order moment to the dynamics of c , $\mathbf{m}$, and $\mathbf{Q}$ and retaining only the leading

order in the fields and their derivatives, we obtain the following equations of motion for c , $\mathbf{m}$, and $\mathbf{Q}$ in three dimensions:

$$(\partial_t + U_\alpha \nabla_\alpha) c = -\nabla_\alpha m_\alpha, \quad (\text{C1})$$

$$\begin{aligned} (\partial_t + U_\alpha \nabla_\alpha) m_i = & -m_i - \nabla_\alpha \left(Q_{i\alpha} + \frac{1}{3} \delta_{i\alpha} c \right) \\ & + \frac{4}{5} m_\alpha \nabla_\alpha U_i - \frac{1}{5} m_\alpha \nabla_i U_\alpha, \end{aligned} \quad (\text{C2})$$

$$\begin{aligned} (\partial_t + U_\alpha \nabla_\alpha) Q_{ij} = & -Q_{ij} - \frac{1}{5} \left(\nabla_j m_i + \nabla_i m_j - \frac{2}{3} \delta_{ij} \nabla_\alpha m_\alpha \right) + \frac{1}{5} c (\nabla_j U_i + \nabla_i U_j) + \frac{1}{7} \nabla^2 Q_{ij} \\ & + \frac{3}{35} \left(\nabla_i \nabla_\alpha Q_{\alpha j} + \nabla_j \nabla_\alpha Q_{\alpha i} - \frac{2}{3} \delta_{ij} \nabla_\alpha \nabla_\beta Q_{\alpha\beta} \right) - \frac{2}{7} \delta_{ij} Q_{\alpha\beta} \nabla_\alpha U_\beta \\ & + \frac{5}{7} (Q_{i\alpha} \nabla_\alpha U_j + Q_{j\alpha} \nabla_\alpha U_i) - \frac{2}{7} (Q_{i\alpha} \nabla_j U_\alpha + Q_{j\alpha} \nabla_i U_\alpha), \end{aligned} \quad (\text{C3})$$

$$\nabla_i \left(p + \frac{1}{3} c \right) = \nabla^2 U_i - 5 \frac{n}{n_c} \nabla_\beta Q_{i\beta}, \quad (\text{C4})$$

$$\nabla_i U_i = 0. \quad (\text{C5})$$

Here, p and $\mathbf{U}$ are, respectively, the fluid pressure and velocity, indices denote Cartesian spatial coordinates, and we assume summation over repeated indices. The crucial point is that these equations have been made dimensionless based on the following rescalings: (i) time is rescaled by λ^{-1} , (ii) length is rescaled by $\ell_p = v_s/\lambda$, (iii) fluid velocity is rescaled by v_s , and (iv) c , $\mathbf{m}$, and $\mathbf{Q}$ are rescaled by the

average microswimmer density n . As can be seen by visual inspection, when using this nondimensionalization, the suspension's dynamics are controlled by a single dimensionless parameter occurring in the Stokes equation (C4), namely n/n_c , which encodes the distance from the onset of active turbulence, with n_c for an infinite system given by Eq. (1). As discussed in the main text, a crucial consequence of this observation is that *any* length scale $\tilde{\ell}^*$ emerging as a result of interactions between microswimmers can be written in dimensionless form as a function of this single parameter, i.e., $\tilde{\ell}^* = f(n/n_c)$, where f is an unknown function.