Silent Flocks: Constraints on Signal Propagation Across Biological Groups

Andrea Cavagna,[1,2,3,*] Irene Giardina,[1,2,3] Tomas S. Grigera,[4] Asja Jelic,[1,2] Dov Levine,[5,3] Sriram Ramaswamy,[6,†] and Massimiliano Viale[1,2]
[1]*Istituto Sistemi Complessi, Consiglio Nazionale delle Ricerche, UOS Sapienza, 00185 Rome, Italy*
[2]*Dipartimento di Fisica, Università Sapienza, 00185 Rome, Italy*
[3]*Initiative for the Theoretical Sciences, The Graduate Center, CUNY, New York, New York 10016 USA*
[4]*Instituto de Investigaciones Fisicoquímicas Teóricas y Aplicadas (INIFTA) and Departamento de Física, Facultad de Ciencias Exactas, Universidad Nacional de La Plata, Casilla de Correo 16, Sucursal 4, 1900 La Plata, Argentina CONICET La Plata, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina*
[5]*Department of Physics, Technion-IIT, 32000 Haifa, Israel*
[6]*TIFR Centre for Interdisciplinary Sciences, 21 Brundavan Colony, Osman Sagar Road, Narsingi, Hyderabad 500 075, India*
(Received 21 October 2014; revised manuscript received 4 February 2015; published 27 May 2015)

Experiments find coherent information transfer through biological groups on length and time scales distinctly below those on which asymptotically correct hydrodynamic theories apply. We present here a new continuum theory of collective motion coupling the velocity and density fields of Toner and Tu to the inertial spin field recently introduced to describe information propagation in natural flocks of birds. The long-wavelength limit of the new equations reproduces the Toner-Tu theory, while at shorter wavelengths (or, equivalently, smaller damping), spin fluctuations dominate over density fluctuations, and second-sound propagation of the kind observed in real flocks emerges. We study the dispersion relation of the new theory and find that when the speed of second sound is large, a gap in momentum space sharply separates first- from second-sound modes. This gap implies the existence of silent flocks, namely, of medium-sized systems across which information cannot propagate in a linear and underdamped way, either under the form of orientational fluctuations or under that of density fluctuations, making it hard for the group to achieve coordination.

DOI: 10.1103/PhysRevLett.114.218101 PACS numbers: 87.23.Cc, 05.65.+b, 47.54.-r, 87.18.Hf

Models of self-propelled particles, where dynamical equations for the individual velocities and positions are specified for each particle [1–4], offer a microscopic description of a variety of active matter systems [5,6], from granular materials [7], to bacterial colonies [8] and animal groups [9]. By coarse graining the microscopic models [10,11], it is possible to derive the hydrodynamic equations describing the dynamics of the velocity and density fields at large scales of length and time [12–17]. The minimal model of collective motion is the Vicsek model [1]; its continuous formulation has been provided by the elegant hydrodynamic theory of Toner and Tu [12].

The power of the hydrodynamic approach lies in the unambiguous choice of variables—only those whose time scale diverges in the limit of infinite system size and wave number $k \to 0$. Once these hydrodynamic variables determined by conservation laws and broken symmetries are identified, the theory is independent of the details of the microscopic dynamics. Natural systems, however, are often far from such limits and exhibit collective phenomena over intermediate scales. A notable case is that of bird flocks, which perform collective turns on so short a time scale that mutual positions remain almost the same, and the coupling between density and velocity fluctuations is weak [18]. To make a comparison with the data, it is essential not to restrict to the $k \to 0$ limit. This forces us to give up universality and to resort to experimental data in order to decide what is relevant and what is not in a finite-size theory of collective motion. The scales involved still contain a large number of birds, though, so a coarse-grained approach remains appropriate.

It has been experimentally found in Ref. [18] that in order to describe information transfer through natural (and, thus, finite) flocks of birds, it is crucial to take into account inertial effects. In particular, it is necessary to associate to the velocity a new quasiconserved variable, the spin [18]. The spin is the generalized momentum generating the local rotations of the velocity field. Spin fluctuations transport across the flock the orientational information responsible for the turn. The spin has an associated inertia, which is formally to the spin what standard mass is to linear momentum.

The inertial spin model (ISM) [19] couples the dynamics of the velocity to that of the spin. At very large scales (or, equivalently, for very large damping), the inertial effects in the ISM are irrelevant, but over finite scales they become essential. The nature of this crossover is not known, though, because the ISM has been analytically studied only in the short-time limit of negligible density fluctuations [19]. Here we address this point by introducing a new set of continuous equations corresponding to the dynamical field description of the ISM. As expected, for $k \to 0$ the new field equations reproduce the Toner-Tu theory [12].

However, for nonzero k, and, therefore, finite length and time scales, we find a new and rich phenomenology. The most surprising result is the emergence of a range of wave numbers over which no mode is propagative, showing that propagation phenomena in flocks are possible only in certain size regimes.

Before we proceed, a remark is in order. We will consider the hydrodynamic consequences of a minimal modification of the Turner-Tu theory [12], in which a variable that is not formally slow but is quasiconserved (the spin) is promoted to the status of a true slow variable. Of course, more intricate models can be proposed for bird flocks. Those that introduce rule changes on a local scale will not alter the qualitative long-wavelength physics; on the other hand, theories involving long-range couplings, like the marginal opacity idea of Ref. [20] or introducing an additional continuous broken symmetry, such as the lattice formation of Ref. [21] (see, also, Ref. [22]), can do so. We finally notice that the additional variable used in the anticipation dynamics of Ref. [23] is akin to our spin.

We aim to write the hydrodynamic theory corresponding to the microscopic ISM introduced in Ref. [19]. To do this, we follow the Ginzburg-Landau approach used by Toner and Tu (TT) in Ref. [12]; namely, we identify the underlying symmetries and crucial couplings of the microscopic model and build the minimal continuous theory compatible with those. It has been shown in Ref. [19] that the spin-overdamped limit of the ISM coincides with the Vicsek model [24]. Because the Vicsek model is for the TT hydrodynamic theory what the ISM is for the new theory, we ask that the spin-overdamped limit of our new equations must be equal to TT equations. Using these guidelines, we propose the following dynamical field theory:

$$D_t\mathbf{v} = \frac{1}{\chi}\mathbf{s}\times\mathbf{v} - \nabla P - \frac{\delta V}{\delta \mathbf{v}}, \tag{1a}$$

$$D_t\mathbf{s} = \frac{\mathcal{J}}{v_0^2}\mathbf{v}\times\nabla^2\mathbf{v} - \frac{\eta}{\chi}\mathbf{s}, \tag{1b}$$

$$\partial_t\rho = -\nabla\cdot(\rho\mathbf{v}). \tag{1c}$$

Some of the terms in Eq. (1) are the same as in the TT theory [12,25]: $\mathbf{v}$ and ρ are the velocity and density fields, the material derivative is defined as $D_t = \partial_t + \lambda\mathbf{v}\cdot\nabla$, where λ breaks the Galilean invariance (we could allow for different λ in the $\mathbf{v}$ and $\mathbf{s}$ equations), the pressure $P(\rho)$ is a function of the density, and the confining potential is $V(\mathbf{v}) = \int d^3r[-(\alpha/2)v^2 + (\beta/2)(\mathbf{v}\cdot\mathbf{v})^2]$ with $\alpha/\beta = v_0^2$. The novel ingredients coming from the ISM are the spin field $\mathbf{s}$, its associated inertia χ, and the spin-velocity coupling $\mathbf{s}\times\mathbf{v}$. This cross product indicates that $\mathbf{s}$ is the generator of the rotations of $\mathbf{v}$, as well as of any other field f. This property is expressed by the Poisson bracket,

$$\{s, f\} = \frac{df}{d\varphi}, \tag{2}$$

where $s = |\mathbf{s}|$, and φ is the phase parametrizing rotations in the plane orthogonal to $\mathbf{s}$ [19]. Equation (1b) is the core of the new theory, as it reinstates inertial effects: the alignment force $\mathcal{J}\nabla^2\mathbf{v}$ acts now on $\dot{\mathbf{s}}$ rather than on $\dot{\mathbf{v}}$, as in the Toner-Tu theory ($\mathcal{J}$ is the alignment coupling [26]). The damping term $-\eta\mathbf{s}$ guarantees that in absence of forces, the spin relaxes to zero. Note the precise formal resemblance of Eq. (1) to the coupled dynamics of the direct and staggered magnetizations in the Heisenberg antiferromagnet [27,28] and to the rotor hydrodynamics [29]. Finally, for simplicity, we have disregarded diffusion terms of the form $\partial_t f = \Gamma\nabla^2 f$, as their effect on the dispersion relation of the linearized theory amounts to a renormalization of the parameters (these terms may have an impact, though, at the nonlinear level).

An explicit coarse-graining path from the microscopic ISM to the hydrodynamic equations has been adopted in Ref. [30]. Such route requires an approximated closure scheme and possibly for this reason the equations of Ref. [30] as derived from microscopics lack some of the terms that we obtain here on the basis of symmetries; in particular, the term $\mathbf{v}\times\nabla^2\mathbf{v}$, which, as we shall see, is crucial for the propagating spin waves, is not microscopically derived in Ref. [30], although it is present in its numerics. We also note that Ref. [30], rather than focusing on the dispersion relation as we do here, investigates the possible mechanisms for instabilities when the spin inertia is increased.

As usual with viscous dynamics, when the dissipation η is very high compared to the inertia χ, momentum becomes irrelevant, and one obtains the overdamped limit [31]. To study this case, one must rescale the time $t\to\eta^{-1}t$ (and all other dimensional quantities accordingly [32]) and take the limit $\chi/\eta^2\to 0$. When this is done, the spin $\mathbf{s}$ can be eliminated, giving

$$D_t\mathbf{v} = \mathcal{J}\nabla^2\mathbf{v} - \nabla P - \frac{\delta V}{\delta\mathbf{v}}, \tag{3a}$$

$$\partial_t\rho = -\nabla\cdot(\rho\mathbf{v}). \tag{3b}$$

Equations (3) are the same as the TT equations [12,14] in their simplest form, with $\mathcal{J}$ playing the role of the kinematic viscosity or stiffness depending on whether one views $\mathbf{v}$ as a velocity or an orientation [16]. Hence, the spin-overdamped limit of our new field equations gives the TT theory, consistent with the fact that, in the same limit, the ISM is identical to the Vicsek model [19].

To check for propagating modes, we study the linear expansion of Eqs. (1) in the broken-symmetry phase and in the limit of low noise, i.e., high polarization. We consider fluctuations around the equilibrium values of $\mathbf{v}$, ρ, and P: $\mathbf{v} = v_0\check{\mathbf{n}} + \delta\mathbf{v}$, $\rho = \rho_0 + \delta\rho$, and $P = P_0 + \sigma\delta\rho$, where $\sigma = \partial_\rho P(\rho=\rho_0)$. Apart from factors of density, σ, thus, acts as a bulk modulus (see, also, Ref. [16]). We perform a

Galilean transformation to a frame where the average velocity is zero. Since λ is known to be close to 1 [14], we neglect terms proportional to $\lambda - 1$. We introduce the projections of $\delta\mathbf{v}$ in the directions parallel and perpendicular to the direction of motion $\check{\mathbf{n}}$: $\delta\mathbf{v}_\parallel = (\check{\mathbf{n}}\cdot\delta\mathbf{v})\check{\mathbf{n}}$; $\delta\mathbf{v}_\perp = \delta\mathbf{v} - \delta\mathbf{v}_\parallel$. As in any phase with a broken continuous symmetry [29], the longitudinal fluctuations $\delta\mathbf{v}_\parallel$ will relax rapidly compared to the Nambu-Goldstone mode $\delta\mathbf{v}_\perp$ because the potential V in Eq. (1) is flat in the transverse direction. We, therefore, neglect $\delta\mathbf{v}_\parallel$. Finally, we study the equations in the planar case, in which $\delta\mathbf{v}_\parallel$, $\delta\mathbf{v}_\perp$, and $\mathbf{s}$ are scalars (this case does not have any qualitative difference with that of a fully 3D order parameter; see Ref. [19]). The linear expansion of Eqs. (1) becomes [32]

$$\partial_t \delta v_\perp = \frac{v_0}{\chi} s - \sigma \partial_\perp \delta\rho, \tag{4a}$$

$$\partial_t s = \frac{\mathcal{J}}{v_0}\nabla^2 \delta v_\perp - \frac{\eta}{\chi} s, \tag{4b}$$

$$\partial_t \delta\rho = -\rho_0 \partial_\perp \delta v_\perp, \tag{4c}$$

where $\nabla^2 = \partial_\parallel^2 + \partial_\perp^2$. Before studying the existence of propagating modes in Eq. (4), we consider two limiting cases.

The TT limit of overdamping of the spin $\chi/\eta^2 \to 0$ for Eqs. (4) gives

$$\partial_t \delta v_\perp = \mathcal{J}\nabla^2 \delta v_\perp - \sigma \partial_\perp \delta\rho, \tag{5a}$$

$$\partial_t \delta\rho = -\rho_0 \partial_\perp \delta v_\perp. \tag{5b}$$

We work in polar coordinates in momentum space: θ is the angle between $\mathbf{k}$ and the direction of motion of the flock (or longitudinal direction) $k_\parallel = k\cos\theta$, $k_\perp = k\sin\theta$. Introducing the speed of *first sound* $c_1^2 \equiv \rho_0\sigma$ and the damping time $\tau_1 \equiv 2/k^2\mathcal{J}$, the frequencies are given by

$$\omega_\pm = -i/\tau_1 \pm c_1 k\sqrt{\sin^2\theta - k^2/k_1^2}; \quad k_1 \equiv c_1\tau_1 k^2, \tag{6}$$

which is the dispersion relation of Toner and Tu [15]. Propagating modes require a nonzero real part of the frequency, which only happens for $k < k_1|\sin\theta|$. This has two implications: (i) first sound displays *anisotropic* propagation (θ dependence); (ii) first sound is overdamped at short wavelengths (large k). Note that, as in standard fluids, first sound is carried by density fluctuations; however, unlike in standard fluids, it is a consequence of broken symmetry not of momentum conservation [15,16].

On the other hand, taking $\sigma \to 0$ in Eq. (4), the spin decouples from the density, giving

$$\partial_t \delta v_\perp = \frac{v_0}{\chi} s, \tag{7a}$$

$$\partial_t s = \frac{\mathcal{J}}{v_0}\nabla^2 \delta v_\perp - \eta_0 s, \tag{7b}$$

where $\eta_0 \equiv \eta/\chi$ is the reduced viscosity. Introducing the speed of *second sound* $c_2^2 \equiv \mathcal{J}/\chi$ and the damping time $\tau_2 \equiv 2/\eta_0$, the frequencies can be written as

$$\omega_\pm = -i/\tau_2 \pm c_2 k\sqrt{1 - k_2^2/k^2}; \qquad k_2 \equiv 1/c_2\tau_2. \tag{8}$$

This dispersion relation has been obtained in Refs. [18,19] under the approximation that the time scale of collective turns is so short that the network is almost fixed so that density fluctuations and other network distortions [21,22] can be neglected. Unlike the first-sound mode of TT, which travels over density fluctuations, the mode in Eq. (8) describes a density-independent spin wave that is a propagating disturbance purely of the orientations; this mode would propagate also on a fixed lattice, with *zero* density fluctuations. In analogy with the spin-wave theory of superfluidity [27], we call this mode "second sound" [18]. There are two fundamental differences between second sound (8) and first sound (6): (i) the dispersion relation for second sound is *isotropic*, in particular, second sound can propagate also in the parallel direction, whereas first sound cannot; (ii) ω has a real part only for $k > k_2$; hence, second sound is overdamped at long wavelengths (small k).

To understand the crossover between first and second sound, we must study the full linearized equations (4). We have three fields (velocity, spin, and density), and, therefore, three frequency modes given by the solutions of the following dispersion relation [32]:

$$\omega^3 + i\eta_0\omega^2 - (c_1^2k_\perp^2 + c_2^2k^2)\omega - i\eta_0 c_1^2 k_\perp^2 = 0. \tag{9}$$

It is convenient to introduce the dimensionless frequency $\tilde{\omega} \equiv \omega/\eta_0$ and the dimensionless momentum, $\tilde{\mathbf{k}} \equiv c_1\mathbf{k}/\eta_0$. Once this is done, we find that the dispersion relation only depends on one key parameter $\epsilon \equiv c_2/c_1$,

$$\tilde{\omega}^3 + i\tilde{\omega}^2 - \tilde{k}^2(\sin^2\theta + \epsilon^2)\tilde{\omega} - i\tilde{k}^2\sin^2\theta = 0. \tag{10}$$

The parameter ϵ is the second-to-first-sound speed ratio; much of the propagation properties of the new theory depend on ϵ, namely, on how fast second sound is compared to first. Hence, the balance between the efficiencies in transporting orientational vs density information across the flock rules the dispersion relation. After a little algebra [32], one finds that there is a critical value of the speed ratio $\epsilon_c = \sqrt{8}$ separating two very different regimes.

We first analyze the small speed ratio regime, $\epsilon < \epsilon_c$. When second-sound speed is not too large compared to first sound, we have the situation depicted in Fig. 1 (left): there is a region along the longitudinal momentum axis where the real part of the frequency is zero for all modes so that no propagation can take place. In the rest of the $\mathbf{k}$ plane, two modes (out of three) have $\mathrm{Re}\,\omega(k) \neq 0$ so that propagation occurs. Let us fix a direction θ of the wave vector $\mathbf{k}$ and follow a path by increasing the modulus k. If θ is large

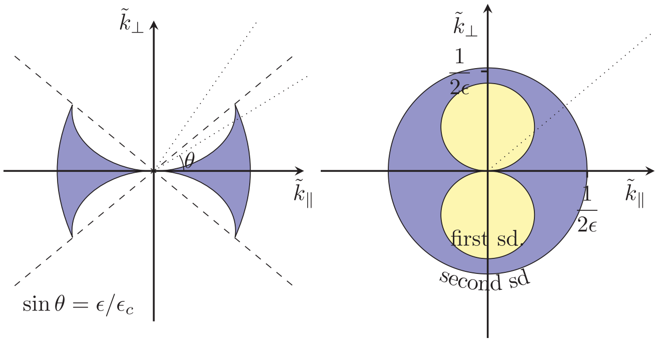

FIG. 1 (color). Left: *Small speed ratio*, $\epsilon < \epsilon_c$. In the overdamped—nonpropagating—zone (blue), we have $\mathrm{Re}\tilde{\omega} = 0$, while in the propagating zone (white) $\mathrm{Re}\tilde{\omega} \neq 0$. The dotted lines indicate two paths along which k may be changed. The lower path characterized by $\sin\theta < \epsilon/\epsilon_c$ crosses the nonpropagating region, giving rise to a gap (Fig. 2, top, red line). The overdamped region just touches the dashed lines marking $\sin\theta = \epsilon/\epsilon_c$. Right: *Large speed ratio*, $\epsilon > \epsilon_c$. The two propagating zones $\mathrm{Re}\tilde{\omega} \neq 0$ are now completely separated by an overdamped ring (blue). Any path in momentum space connecting the region of first-sound propagation (yellow) with that of second-sound propagation (white) must cross the overdamped ring, giving rise to a gap between first and second sound (Fig. 2, bottom).

enough ($\sin\theta > \epsilon/\epsilon_c$), the real part of $\omega(k)$ is always nonzero so that there is propagation at all wavelengths [Fig. 2 (top)]. On the other hand, if θ is small ($\sin\theta < \epsilon/\epsilon_c$), the path crosses the overdamped region, and a *gap* emerges: the propagating regimes for small and large k are separated from each other by a nonpropagating region at intermediate k [Fig. 2 (top)]. This gap separates the first-sound region at low k from the second-sound region at large k (see Ref. [32] for the $k \to 0$ vs $k \to \infty$ exact solutions). For large θ, there is hybridization of first and second sound, and the crossover from one mode to the other is smooth.

Let us now turn to the large-speed-ratio regime, $\epsilon > \epsilon_c$. When ϵ increases, the nonpropagating region grows in size: the tips of the left and right wedges approach and eventually touch each other for $\epsilon = \epsilon_c$, sealing the first-sound pocket at small k. For $\epsilon > \epsilon_c$, the situation is the one shown in Fig. 1 (right): the two propagating regions are now completely disconnected. This means that when we plot the real part of the frequency as a function of k, we are bound to find a nonpropagating gap between first and second sound, no matter what path we follow in momentum space [Fig. 2 (bottom)]. When the second-sound speed c_2 is much larger than the first-sound speed c_1 ($\epsilon > \epsilon_c$), spin fluctuations propagate much faster than density fluctuations. Hence, in the $\epsilon > \epsilon_c$ regime, the turning information propagates on a much shorter time scale than density fluctuations; for this reason it is justified to assume that the network is fixed during propagation. This is the physical meaning of the separation between first and second sound for $\epsilon > \epsilon_c$ and the reason why experimental data on turning flocks are in agreement with the fixed network approximation of Ref. [18].

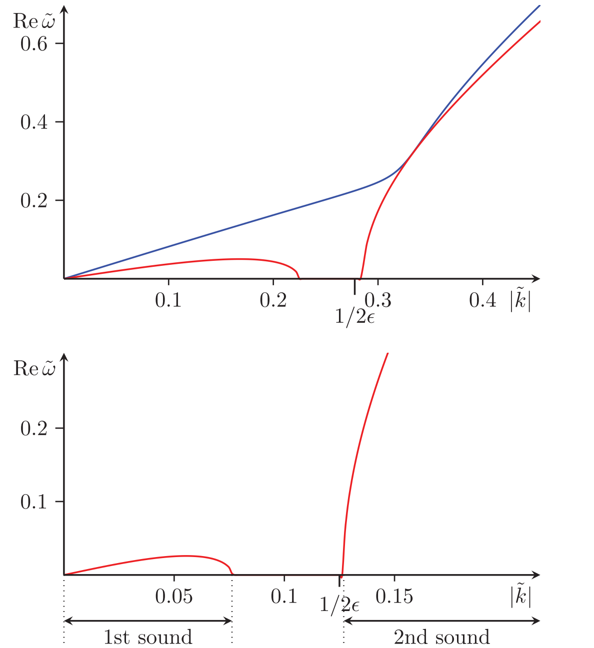

FIG. 2 (color). Top: *Small speed ratio*, $\epsilon < \epsilon_c$. Real part of the frequency vs $|\tilde{k}|$ along two different directions (dotted lines of Fig. 1, left). For $\sin\theta > \epsilon/\epsilon_c$ (blue), there is no gap, and a propagating mode exists at all wavelengths. On the other hand, for $\sin\theta < \epsilon/\epsilon_c$ (red), an overdamped gap emerges, separating first sound (low $\tilde{k}$) from second sound (large $\tilde{k}$). Bottom: *Large speed ratio*, $\epsilon > \epsilon_c$. Real part of the frequency vs $|\tilde{k}|$ at one given value of θ (dotted line in Fig. 1, right). A nonpropagating gap between first and second sound is found at any θ. For $\theta = 0$, the gap extends down to $k = 0$. The lower band edge of second sound occurs at $\tilde{k} \sim 1/2\epsilon$, that is, $k = \eta_0/2c_2 = k_2$, consistent with the second-sound limit (8).

In a system of finite-size L, a nonzero real part of the asymptotic small-k frequency is not enough to grant information transfer. Modes are damped with a characteristic time $\tau(k) = 1/\mathrm{Im}\omega(k)$, and cross-system propagation only occurs when the distance traveled by the signal before damping is larger than L. By dimensional analysis, this distance is $c_1\tau_1 \sim k_1/k^2$ for first sound, that is, for density fluctuations, and $c_2\tau_2 \sim 1/k_2$ for second sound, that is, for directional information [Eqs. (6)–(8)]. Moreover, the maximum wavelength traveling through the system cannot exceed its size. These two conditions give

$$1/k < L < k_1/k^2; \qquad 1/k < L < 1/k_2, \tag{11}$$

for first and second sound, respectively. By collapsing the two sides of each inequality, we obtain that cross-system propagation can only occur if $L > 1/k_1$ for first sound and if $L < 1/k_2$ for second sound. Therefore, if there is a gap in momentum space, namely, if $k_1 < k_2$, we obtain a corresponding gap in L for $1/k_1 < L < 1/k_2$. We conclude that there is a regime of medium-sized flocks that are "silent": no propagative signal can cross the system at any wavelength. In silent flocks, neither directional nor density disturbances can propagate in a wavelike manner, namely, linearly and weakly damped. Using the full dispersion relation and, therefore, the true phase velocity $c(k)$ and damping time $\tau(k)$ does not change qualitatively the dimensional argument [32]. In fact, it is possible to show that the gap in L appears even *before* the gap in k in the region where $\mathrm{Re}\,\omega(k)$ has a minimum.

Second sound is essential to transfer directional information across natural flocks [18]. The fact that second sound is damped in large systems may be responsible for an upper cutoff in the size of flocks performing collective turns. Very large flocks exist, but they may have troubles to collectively change direction of motion. Even though we have no data on huge flocks, i.e., of the order 10^4 individuals or larger, our anecdotal experience in the field agrees with this conclusion. More speculatively, a silent regime at intermediate sizes, where no information whatsoever can propagate (not spin or density fluctuations), might render such flocks unviable, suggesting a new reason why size control might be an important consideration in the evolution of biological groups. Unlike previous theoretical predictions only detectable in the hydrodynamic limit, our results are valid even at small-to-moderate scales: a broad range of parameters exists for which a flock could be smaller than the scale above which first sound is propagative and yet too large for second sound to make it across the whole system. Flocks in this size range, thus, lack a clean, system-spanning signaling mechanism.

A. C. acknowledges US-AFOSR Grant No. FA95501010250 (through the University of Maryland), I. G. Grants No. 257126 from ERC and Seed-Artswarm from IIT. S. R. acknowledges support from a J. C. Bose Fellowship, the hospitality of the Initiative for Theoretical Sciences at the CUNY Graduate Center, the support of the Kavli Institute for Theoretical Physics under Grant No. NSF PHY11-25915, and discussions with M. C. Marchetti, X. Yang, and J. Toner.

*Corresponding author.
andrea.cavagna@roma1.infn.it
†On leave from Department of Physics, Indian Institute of Science, Bangalore 560 012, India.

[1] T. Vicsek, A. Czirók, E. Ben-Jacob, I. Cohen, and O. Shochet, Phys. Rev. Lett. **75**, 1226 (1995).
[2] G. Grégoire and H. Chaté, Phys. Rev. Lett. **92**, 025702 (2004).
[3] C. K. Hemelrijk and H. Hildenbrandt, PLoS One **6**, e22479 (2011).
[4] P. Romanczuk, M. Bär, W. Ebeling, B. Lindner, and L. Schimansky-Geier, Eur. Phys. J. Spec. Top. **202**, 1 (2012).
[5] T. Vicsek and A. Zafeiris, Phys. Rep. **517**, 71 (2012).
[6] A. Cavagna and I. Giardina, Annu. Rev. Condens. Matter Phys. **5**, 183 (2014).
[7] I. S. Aranson and L. S. Tsimring, Rev. Mod. Phys. **78**, 641 (2006).
[8] X. Chen, X. Dong, A. Be'er, H. L. Swinney, and H. P. Zhang, Phys. Rev. Lett. **108**, 148101 (2012).
[9] I. D. Couzin and J. Krause, Adv. Study Behav. **32**, 1 (2003).
[10] E. Bertin, H. Chaté, F. Ginelli, S. Mishra, A. Peshkov, and S. Ramaswamy, New J. Phys. **15**, 085032 (2013).
[11] A. Peshkov, E. Bertin, F. Ginelli, and H. Chaté, Eur. Phys. J. Spec. Top. **223**, 1315 (2014).
[12] J. Toner and Y. Tu, Phys. Rev. Lett. **75**, 4326 (1995).
[13] Y. Tu, J. Toner, and S. Ramaswamy, Ann. Phys. (Amsterdam) **318**, 170 (2005).
[14] Y. Tu, J. Toner, and M. Ulm, Phys. Rev. Lett. **80**, 4819 (1998).
[15] J. Toner and Y. Tu, Phys. Rev. E **58**, 4828 (1998).
[16] S. Ramaswamy, Annu. Rev. Condens. Matter Phys. **1**, 323 (2010).
[17] M. C. Marchetti, J. F. Joanny, S. Ramaswamy, T. B. Liverpool, J. Prost, M. Rao, and R. Aditi Simha, Rev. Mod. Phys. **85**, 1143 (2013).
[18] A. Attanasi *et al.*, Nat. Phys. **10**, 691 (2014).
[19] A. Cavagna *et al.*, J. Stat. Phys. **158**, 601 (2015).
[20] D. J. G. Pearce, A. M. Miller, G. Rowlands, and M. S. Turner, Proc. Natl. Acad. Sci. U.S.A. **111**, 10422 (2014).
[21] E. Ferrante, A. Emre Turgut, M. Dorigo, and C. Huepe, Phys. Rev. Lett. **111**, 268302 (2013).
[22] R. Lahiri and S. Ramaswamy, Phys. Rev. Lett. **79**, 1150 (1997) study the dynamics of the broken-symmetry mode of a lattice drifting under an external force. The relation of this to the spontaneously drifting case is studied by S. Banerjee, A. Maitra, M. C. Marchetti, S. Ramaswamy, and J. Toner (to be published)
[23] A. Morin, J.-B. Caussin, C. Eloy, and D. Bartolo, Phys. Rev. E **91**, 012134 (2015).
[24] The theory we are about to introduce gives propagating modes even in the "overdamped" limit. This odd behavior is due to the fact that the infinite spin viscosity limit of the ISM (a limit normally called overdamped) reproduces the Vicsek model, which has the propagating modes of Toner and Tu. To avoid this ambiguity, we have decided to term the large η limit, "spin overdamped" rather than simply overdamped.
[25] The term $\nabla \times \mathbf{v}$ included in the variant of Eq. (1b) in Ref. [30] can be rewritten as $\mathbf{v} \cdot \nabla\varphi$, where φ is the phase parametrizing rotations of $\mathbf{v}$ on the plane orthogonal to $\mathbf{s}$. In a frame comoving with the flock, as employed in this paper, and taking all the λ's to be unity, this term is eliminated from the linearized dynamics about the ordered phase.
[26] In the microscopic model $\mathcal{J} = a^2 J$, where a is the lattice spacing and J the microscopic (bare) alignment strength [19].
[27] B. I. Halperin and P. C. Hohenberg, Phys. Rev. **188**, 898 (1969).
[28] G. F. Mazenko, M. J. Nolan, and R. Freedman, Phys. Rev. B **18**, 2281 (1978).
[29] P. M. Chaikin and T. C. Lubensky, *Principles of Condensed Matter Physics* (Cambridge University Press, New Delhi, 1998), Chap. 8.
[30] X. Yang and M. C. Marchetti, arXiv:1410.1827.
[31] R. Zwanzig, *Nonequilibrium Statistical Mechanics* (Oxford University Press, Oxford, 2001).
[32] See the Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevLett.114.218101 for the detailed algebraic passages.