Birth, Death, and Flight: A Theory of Malthusian Flocks

John Toner

Department of Physics and Institute of Theoretical Science, University of Oregon, Eugene, Oregon 97403, USA (Received 23 August 2011; published 23 February 2012)

I study "Malthusian flocks": moving aggregates of self-propelled entities (e.g., organisms, cytoskeletal actin, microtubules in mitotic spindles) that reproduce and die. Long-ranged order (i.e., the existence of a nonzero average velocity $\langle \vec{v}(\vec{r},t) \rangle \neq \vec{0}$) is possible in these systems, even in spatial dimension d = 2. Their spatiotemporal scaling structure can be determined exactly in d = 2; furthermore, they lack both the longitudinal sound waves and the giant number fluctuations found in immortal flocks. Number fluctuations are very *persistent*, and propagate along the direction of flock motion, but at a different speed.

DOI: 10.1103/PhysRevLett.108.088102

PACS numbers: 87.18.Gh, 05.65.+b, 64.70.qj

Flocking [1]—the coherent motion of large numbers of organisms—spans a wide range of length scales: from kilometers (herds of wildebeest) to microns (microorganisms [2,3]; mobile macromolecules in living cells [4,5]). It is also [6] a dynamical version of ferromagnetic ordering. A "hydrodynamic" theory of flocking [7] shows that, unlike equilibrium ferromagnets [8], flocks *can* spontaneously break a continuous symmetry (rotation invariance) by developing long-ranged order, (i.e., a nonzero average velocity $\langle \vec{v}(\vec{r}, t) \rangle \neq \vec{0}$) in spatial dimensions d = 2, even with only short-ranged interactions.

Many quantitative predictions of the hydrodynamic theory, including the stability of long-ranged order in d = 2, the existence of propagating, dispersionless sound modes with nontrivial direction dependence of their speeds, and the presence of anomalously large number fluctuations, agree with numerical simulations [7,9], and experiments on self-propelled molecules [10].

However, a recent reanalysis [11] of this hydrodynamic theory has cast doubt on the claim that exact scaling exponents could be determined for flocks in d = 2. This is due to the erroneous neglect in [7] of nonlinearities arising from the local number density dependences of various phenomenological parameters; these nonlinearities could change the scaling exponents from those claimed in [7].

In this Letter, I show that these difficulties can be avoided in flocks *without* number conservation [12]. A number of real systems lack number conservation, including growing bacteria colonies [13], and "treadmilling" molecular motor propelled biological macromolecules in a variety of intracellular structures, including the cytoskleton, and mitotic spindles [4,5], in which molecules are being created and destroyed as they move. Hence, the study of such systems is not only convenient, but experimentally relevant. The most obvious example of flocking—namely, actual birds—is clearly *not* a good example of a Malthusian flock. To avoid any confusion on this point, I will henceforth use the term "boid" [1], rather than "bird", to refer to the moving, self-propelled entities that make up the flock.

I will treat systems with the same symmetries as were considered in earlier work on immortal flocks [7]: orientationally ordered, translationally disordered phases (i.e., phases with $\langle \vec{v}(\vec{r}, t) \rangle \neq \vec{0}$ that are uniform in space and time) in systems with short-ranged, rotation invariant interactions, moving through (or on, in d = 2) a *fixed* background medium that breaks Galilean invariance.

Since my treatment is hydrodynamic, it only describes large systems at long length and time scales. However, it becomes asymptotically exact in that limit.

The removal of number conservation leads to profound changes. The sound modes of number conserving (hereafter "immortal") flocks disappear, and are replaced by longitudinal velocity fluctuations which drift in the direction of flock motion with a speed $\gamma \neq v_0$, where v_0 is the mean speed of the flock. While drifting, these modes also spread diffusively along the direction of flock motion, and hyperdiffusively perpendicular to that direction.

In both Malthusian and immortal flocks, anomalous hydrodynamics stabilizes long-ranged orientational order (i.e., $\langle \vec{v}(\vec{r}, t) \rangle \neq \vec{0}$) in spatial dimension d = 2. In Malthusian flocks, the order outlives the boids: the persistence time diverges as the number of boids $N \rightarrow \infty$, while the lifetime of the boids remains finite in this limit.

The scaling exponents of the hydrodynamics can be determined *exactly* in spatial dimension d = 2 for Malthusian flocks, while, as discussed above, those in immortal flocks cannot. These exponents are the *dynamical* exponent z for the scaling of time scales $t(L_{\perp}) \propto L_{\perp}^z$ with length scale L_{\perp} perpendicular to the direction of flock motion, an *anisotropy* exponent ζ for the scaling of distances $L_{\parallel}(L_{\perp}) \propto L_{\perp}^{\zeta}$ parallel to the direction of motion with L_{\perp} , and a "roughness" exponent χ relating the scale of velocity fluctuations to L_{\perp} via $\delta v \propto L_{\perp}^{\chi}$. I find that, for Malthusian flocks in spatial dimension d = 2, these exponents are

$$\zeta = \frac{3}{5}, \qquad z = \frac{6}{5}, \qquad \chi = -\frac{1}{5}.$$
 (1)

The velocity field can have long-ranged order, $(\langle \vec{v}(\vec{r},t) \rangle \neq \vec{0})$ in d = 2, because the roughness exponent $\chi(d = 2) < 0$.

Number fluctuations in Malthusian flocks exhibit anomalous *persistence*: the experimentally observable density-density correlation function

$$C_{\rho}(\vec{r},t) \equiv \langle \delta \rho(\vec{r}',t') \delta \rho(\vec{r}'+\vec{r},t'+t) \rangle, \qquad (2)$$

where $\delta \rho(\vec{r}, t) \equiv \rho(\vec{r}, t) - \rho_0$ is the departure of the local number density of boids $\rho(\vec{r}, t)$ from its mean value ρ_0 , decays algebraically with time at a fixed point in space:

$$C_{\rho}(\vec{r} = \vec{0}, t) \propto |t|^{-4},$$
 (3)

in spatial dimensions d = 2, while for a point translating along the direction \hat{x}_{\parallel} of flock motion at the "drift" speed γ the decay is even slower: in both 2 and 3 spatial dimensions, I find

$$C_{\rho}(\vec{r} = \gamma t \hat{x}_{\parallel}, t) \propto |t|^{-2}.$$
(4)

These should be contrasted with the exponential decay with time of density fluctuations that occurs in a *disordered* Malthusian flock (i.e., one in which $\langle \vec{v} \rangle = \vec{0}$).

Since C_{ρ} and C_{v} can be constructed from *any* set of high-resolution images of a moving flock, as has been done for flocks of starlings in Ref. [14] and for a related correlation function of bacteria in [13], it should not be difficult to test these predictions.

I will now outline the derivation of these results.

My starting equation of motion for the velocity is exactly that of an immortal flock [15]:

$$\begin{aligned} \partial_t \vec{v} + \lambda_1 (\vec{v} \cdot \vec{\nabla}) \vec{v} + \lambda_2 (\vec{\nabla} \cdot \vec{v}) \vec{v} + \lambda_3 \vec{\nabla} (|\vec{v}|^2) \\ &= \alpha \vec{v} - \beta |\vec{v}|^2 \vec{v} - \vec{\nabla} P_1 - \vec{v} [\vec{v} \cdot \vec{\nabla} P_2(\rho, |\vec{v}|)] \\ &+ D_B^o \vec{\nabla} (\vec{\nabla} \cdot \vec{v}) + D_T \nabla^2 \vec{v} + D_2 (\vec{v} \cdot \vec{\nabla})^2 \vec{v} + \vec{f}, \end{aligned}$$
(5)

where all of the parameters $\lambda_i (i = 1 \rightarrow 3)$, α , β , D_B^o , $D_{T,2}$ and the "pressures" $P_{1,2}(\rho, |\vec{v}|)$ are, in general, functions of the boid number density ρ and the magnitude $|\vec{v}|$ of the local velocity. I will expand $P_{1,2}(\rho, |\vec{v}|)$ about ρ_0 : $P_i(\rho) = P_i^0 + \sum_{n=1}^{\infty} \sigma_{i,n}(|\vec{v}|)\delta\rho^n$, where i = 1, 2.

In (5), β , D_B^o , D_2 and D_T are all positive, while $\alpha < 0$ in the disordered phase and $\alpha > 0$ in the ordered state.

The α and β terms give \vec{v} a nonzero magnitude $v_0 = \sqrt{\frac{\alpha}{\beta}}$ in the ordered phase. The diffusion constants $D_{B,T,2}$ reflect the tendency of "boids" to follow their neighbors. The \vec{f} term is a random Gaussian white noise, mimicking errors made by the boids, with correlations

$$\langle f_i(\vec{r},t)f_j(\vec{r}',t')\rangle = \Delta\delta_{ij}\delta^d(\vec{r}-\vec{r}')\delta(t-t'), \quad (6)$$

where $\Delta = \text{constant}$, and *i*, *j* label vector components. The "anisotropic pressure" $P_2(\rho, |\vec{v}|)$ in (5) is only allowed due to the nonequilibrium nature of the flock; in an equilibrium fluid such a term is forbidden by Pascal's Law. In earlier work [7] this term was ignored.

Note that (5) is *not* Galilean invariant; it holds only in the frame of the fixed medium through or on which the creatures move.

I now need an equation of motion for ρ . In immortal flocks, this is just the usual continuity equation of compressible fluid dynamics. For Malthusian flocks, it must also include the effects of birth and death. As first noted by Malthus [16], *any* collection of entities that is reproducing and dying can only reach a nonzero steady state population density if the death rate exceeds the birth rate for population densities greater than the steady state density, and the converse for population densities less than the steady state density [17]. This "Malthusian" condition implies that the net, local growth rate of number density in the absence of motion, which I will call $g(\rho)$ —vanishes at some fixed point density ρ_0 , with larger densities decreasing [i.e., $g(\rho > \rho_0) < 0$], and smaller densities increasing [i.e., $g(\rho < \rho_0) > 0$].

The equation of motion for the density is now simply

$$\partial_t \rho + \nabla \cdot (\vec{v}\rho) = g(\rho).$$
 (7)

Note that in the absence of birth and death, $g(\rho) = 0$, and Eq. (7) reduces to the usual continuity equation, as it should, since "boid number" is then conserved.

Since birth and death quickly restore the fixed point density ρ_0 , I will write $\rho(\vec{r}, t) = \rho_0 + \delta\rho(\vec{r}, t)$ and expand both sides of Eq. (7) to leading order in $\delta\rho$. This gives $\rho_0 \vec{\nabla} \cdot \vec{v} \approx g'(\rho_0)\delta\rho$, where I have dropped the $\partial_t \rho$ term relative to the $g'(\rho_0)\delta\rho$ term since I am interested in the hydrodynamic limit, in which the fields evolve extremely slowly. This equation can be readily solved to give

$$\delta\rho \simeq \frac{\rho_0 \vec{\nabla} \cdot \vec{v}}{g'(\rho_0)} \equiv -\frac{\Delta D_B^{(1)}}{\sigma_{1,1}} (\vec{\nabla} \cdot \vec{v}), \tag{8}$$

where $\Delta D_B^{(1)}$ is a positive constant, and $\sigma_{1,1}$ is the first expansion coefficient for P_1 . I can now insert this solution (8) for $\delta \rho$ in terms of \vec{v} into the isotropic pressure P_1 ; the resulting equation of motion for \vec{v} is

$$\begin{aligned} \partial_t \vec{v} &+ \lambda_1 (\vec{v} \cdot \vec{\nabla}) \vec{v} + \lambda_2 (\vec{\nabla} \cdot \vec{v}) \vec{v} + \lambda_3 \vec{\nabla} (|\vec{v}|^2) \\ &= \alpha \vec{v} - \beta |\vec{v}|^2 \vec{v} - \vec{v} (\vec{v} \cdot \vec{\nabla} P_2(\rho, |\vec{v}|)) \\ &+ D_B^{(1)} \vec{\nabla} (\vec{\nabla} \cdot \vec{v}) + D_T \nabla^2 \vec{v} + D_2 (\vec{v} \cdot \vec{\nabla})^2 \vec{v} + \vec{f}, \end{aligned}$$
(9)

where I have defined $D_B^{(1)} \equiv D_B^o + \Delta D_B^{(1)}$. Taking the dot product of both sides of (9) with \vec{v} itself, and defining $U(|\vec{v}|) \equiv \alpha(|\vec{v}|, \rho) - \beta(|\vec{v}|, \rho)|\vec{v}|^2$, I obtain

$$\frac{1}{2}(\partial_{t}|\vec{v}|^{2} + (\lambda_{1} + 2\lambda_{3})(\vec{v}\cdot\vec{\nabla})|\vec{v}|^{2}) + \lambda_{2}(\vec{\nabla}\cdot\vec{v})|\vec{v}|^{2}$$

$$= U(|\vec{v}|)|\vec{v}|^{2} - |\vec{v}|^{2}\vec{v}\cdot\vec{\nabla}P_{2} + D_{B}^{(1)}\vec{v}\cdot\vec{\nabla}(\vec{\nabla}\cdot\vec{v})$$

$$+ D_{T}\vec{v}\cdot\nabla^{2}\vec{v} + D_{2}\vec{v}\cdot[(\vec{v}\cdot\vec{\nabla})^{2}\vec{v}] + \vec{v}\cdot\vec{f}.$$
(10)

In the ordered state (i.e., the state in which $\langle \vec{v}(\vec{r}, t) \rangle = v_0 \hat{x}_{\parallel}$), I can expand the \vec{v} equation of motion for small departures $\delta \vec{v}(\vec{r}, t)$ of $\vec{v}(\vec{r}, t)$ from uniform motion with speed v_0 :

$$\vec{v}(\vec{r},t) = (v_0 + \delta v_{\parallel})\hat{x}_{\parallel} + \vec{v}_{\perp}(\vec{r},t),$$
 (11)

where, henceforth \parallel and \perp denote components along and perpendicular to the mean velocity, respectively.

In this hydrodynamic approach, I am interested only in fluctuations $\delta v(\vec{r}, t) \equiv \delta v_{\parallel} \hat{x}_{\parallel} + \vec{v}_{\perp}(\vec{r}, t)$ and $\delta \rho(\vec{r}, t)$ that vary slowly in space and time. Hence, terms involving spatiotemporal derivatives of $\delta v(\vec{r}, t)$ and $\delta \rho(\vec{r}, t)$ are always negligible, in the hydrodynamic limit, compared to terms involving the same number of powers of fields with fewer spatiotemporal derivatives. Furthermore, the fluctuations $\delta v(\vec{r}, t)$ and $\delta \rho(\vec{r}, t)$ can themselves be shown to be small in the long-wavelength limit. Hence, we need only keep terms in (10) up to linear order in $\delta v(\vec{r}, t)$ and $\delta \rho(\vec{r}, t)$. The $\vec{v} \cdot \vec{f}$ term can likewise be dropped.

These observations can be used to eliminate many terms in Eq. (10), and solve for the quantity $U \equiv (\alpha(\rho, |\vec{v}|) - \beta(\rho, |\vec{v}|)|\vec{v}|^2)$; I obtain $U = \lambda_2 \vec{\nabla} \cdot \vec{v} + \vec{v} \cdot \vec{\nabla} P_2$. Inserting this expression for U back into Eq. (9), I find that P_2 and λ_2 cancel out of the \vec{v} equation of motion, leaving, ignoring irrelevant terms:

$$\partial_t \vec{v} + \lambda_1 (\vec{v} \cdot \vec{\nabla}) \vec{v} + \lambda_3 \vec{\nabla} (|\vec{v}|^2) = D_T \nabla^2 \vec{v} + D_B^{(1)} \vec{\nabla} (\vec{\nabla} \cdot \vec{v}) + D_2 (\vec{v} \cdot \vec{\nabla})^2 \vec{v} + \vec{f}.$$
(12)

This can be made into an equation of motion for \vec{v}_{\perp} involving only $\vec{v}_{\perp}(\vec{r}, t)$ itself by projecting perpendicular to the direction of mean flock motion \hat{x}_{\parallel} , and eliminating δv_{\parallel} using $U = \lambda_2 \vec{\nabla} \cdot \vec{v} + \vec{v} \cdot \vec{\nabla} P_2$ and the expansion $U \approx$ $-\Gamma_1 \delta v_{\parallel} - \Gamma_2 \delta \rho$, where I have defined $\Gamma_1 \equiv -(\frac{\partial U}{\partial |\vec{v}|})_{\rho}^{\rho}$ and $\Gamma_2 \equiv -(\frac{\partial U}{\partial \rho})_{|\vec{v}|}^{0}$, with super- or subscripts 0 denoting functions of ρ and $|\vec{v}|$ evaluated at $\rho = \rho_0$ and $|\vec{v}| = v_0$. Doing this, and using (8) for ρ , I obtain

$$\partial_{t}\vec{v}_{\perp} + \gamma \partial_{\parallel}\vec{v}_{\perp} + \lambda_{1}(\vec{v}_{\perp}\cdot\vec{\nabla}_{\perp})\vec{v}_{\perp}$$

$$= D_{T}\nabla_{\perp}^{2}\vec{v}_{\perp} + D_{B}\vec{\nabla}_{\perp}(\vec{\nabla}_{\perp}\cdot\vec{v}_{\perp}) + D_{\parallel}\partial_{\parallel}^{2}\vec{v}_{\perp} + \vec{f}_{\perp},$$
(13)

where I have defined $\gamma \equiv \lambda_1 v_0$, $D_B \equiv D_B^0 + 2v_0\lambda_3(\lambda_2 - \Gamma_2\Delta D_B^{(1)}/\sigma_{1,1})/\Gamma_1$ and $D_{\parallel} \equiv D_T^0 + D_2^0 v_0^2$.

Changing co-ordinates to a new Galilean frame \vec{r}' moving with respect to our original frame in the direction of mean flock motion at speed γ —i.e., $\vec{r}' \equiv \vec{r} - \gamma t \hat{x}_{\parallel}$ —gives

$$\partial_{t}\vec{v}_{\perp} + \lambda_{1}(\vec{v}_{\perp}\cdot\vec{\nabla}_{\perp})\vec{v}_{\perp} = D_{T}\nabla_{\perp}^{2}\vec{v}_{\perp} + D_{B}\vec{\nabla}_{\perp}(\vec{\nabla}_{\perp}\cdot\vec{v}_{\perp}) + D_{\parallel}\partial_{\parallel}^{\prime 2}\vec{v}_{\perp} + \vec{f}_{\perp}.$$
(14)

Ignoring the nonlinear term λ_1 in this equation of motion gives a noisy, anisotropic, vectorial diffusion equation. This can be readily solved for the mode structure and fluctuations by spatiotemporal Fourier transformation, and has d-1 diffusing modes in spatial dimension d. These separate into d-2 "transverse" modes (i.e., modes with \vec{v}_{\perp} perpendicular to \vec{q}_{\perp}), all with the same imaginary eigenfrequency: $-i\omega_T = D_T |\vec{q}_{\perp}|^2 + D_{\parallel} q_{\parallel}^2$. The remaining diffusive mode (the *only* mode in d=2) is "longitudinal" (i.e., has \vec{v}_{\perp} along \vec{q}_{\perp}), with frequency $-i\omega_L = D_{\perp} |\vec{q}_{\perp}|^2 + D_{\parallel} q_{\parallel}^2$, where $D_{\perp} \equiv D_B + D_T$.

Because the dynamics described above is in the Galileanly boosted frame, the dynamics in the original reference frame \vec{r} will have a steady drift at velocity γ superposed on the diffusive motion described above; that is, both eigenfrequencies get γq_{\parallel} added to them.

I can also calculate the real-space velocity fluctuations $\langle |\vec{v}_{\perp}(\vec{r}, t)|^2 \rangle$ in this linearized approximation; I find that, *in this approximation*, this diverges in all $d \leq 2$. This is analogous to the Mermin-Wagner theorem [8] in equilibrium magnets. However, as in immortal flocks [7], this "Mermin-Wagner" result, and all the linearized scaling laws, are invalidated for $d \leq 4$ by the λ_1 term in (14).

To show this here, I will analyze Eq. (14) using the dynamical renormalization group (RG) [18].

The dynamical RG starts by averaging the equations of motion over the short-wavelength fluctuations, i.e., those with support in the "shell" of Fourier space $b^{-1}\Lambda \leq |\vec{q}| \leq \Lambda$, where Λ is an "ultraviolet cutoff", and b is an arbitrary rescaling factor. Then, one rescales lengths, time, and \vec{v}_{\perp} in Eq. (14) according to $\vec{v}_{\perp} = b^{\chi}\vec{v}'_{\perp}$, $\vec{r}_{\perp} = b\vec{r}'_{\perp}$, $r_{\parallel} = b^{\zeta}r'_{\parallel}$, and $t = b^{z}t'$ to restore the ultraviolet cutoff to Λ . This leads to a new equation of motion of the same form as (14), but with "renormalized" values (denoted by primes below) of the parameters given by

$$D'_{B,T} = b^{z-2}(D_{B,T} + \text{graphs}),$$
 (15)

$$D'_{\parallel} = b^{z-2\zeta} (D_{\parallel} + \text{graphs}), \qquad (16)$$

$$\Delta' = b^{z - \zeta - 2\chi + 1 - d} (\Delta + \text{graphs}), \quad (17)$$

$$\lambda_1' = b^{z+\chi-1}(\lambda_1 + \text{graphs}), \qquad (18)$$

where "graphs" denotes contributions from integrating out the short-wavelength degrees of freedom. If we ignore these graphical corrections (valid for λ_1 small), and choose z, ζ , and χ to keep the linear parameters $D_{B,T,\parallel}$ and Δ fixed, Eq. (18) implies that an initially small λ_1 will grow for all $d \leq 4$, meaning the linearized theory.

It is possible to get *exact* exponents in d = 2. This is because the nonlinearity—the λ_1 term—in (14) is a total derivative in d = 2 (specifically, $\frac{\lambda_1}{2} \partial_{\perp} v_{\perp}^2$), since the \perp subspace is one dimensional in d = 2. In contrast, in

immortal flocks, $v \cdot \rho$ nonlinearities arising from the ρ dependence of λ_1 cannot be written as total derivatives, making it impossible to obtain exact exponents, a fact missed by [7]. Here, because the λ_1 term *is* a total \perp derivative, it can only graphically renormalize terms involving \perp derivatives themselves. Hence, the graphical corrections to D_{\parallel} and Δ in Eqs. (16) and (17) vanish. Therefore, at a fixed point, in d = 2,

$$z - 2\zeta = 0, \qquad z - \zeta - 2\chi + 1 - d = z - \zeta - 2\chi - 1 = 0.$$
(19)

There are no graphical corrections λ_1 either, because the equation of motion (14) remains unchanged by the transformation: $\vec{r}_{\perp} \rightarrow \vec{r}_{\perp} - \lambda_1 \vec{v}_1 t$, $\vec{v}_{\perp} \rightarrow \vec{v}_{\perp} + \vec{v}_1$ for arbitrary constant vector $\vec{v}_1 \perp \hat{x}_{\parallel}$. This exact symmetry must continue to hold upon renormalization, with the *same* value of λ_1 . Hence, λ_1 cannot be graphically renormalized. Requiring that $\lambda'_1 = \lambda_1$ in (18), and setting graphs = 0, implies $\chi = 1 - z$ in *all* $d \leq 4$. This and (19) forms three independent equations for the three unknowns χ , z, and ζ , whose solution in d = 2 is (1).

The scaling exponents z, ζ , and χ determine the scaling form of the velocity-velocity autocorrelation function in arbitrary dimension d through the scaling relation [7]:

$$C_{\nu}(\vec{r},t) \equiv \langle \vec{v}_{\perp}(\vec{0},0) \cdot \vec{v}_{\perp}(\vec{r},t) \rangle = |\vec{r}_{\perp}|^{2\chi} G\left(\frac{r_{\parallel}'}{|\vec{r}_{\perp}|^{\zeta}},\frac{t}{|\vec{r}_{\perp}|^{z}}\right)$$
$$= |\vec{r}_{\perp}|^{2\chi} G\left(\frac{r_{\parallel}-\gamma t}{|\vec{r}_{\perp}|^{\zeta}},\frac{t}{|\vec{r}_{\perp}|^{z}}\right), \tag{20}$$

where the second equality follows from scaling arguments applied to the boosted equation of motion (14), and the third arises from undoing the boost. Here G(u, w) is a scaling function, with scaling arguments $u \equiv \frac{r_{\parallel} - \gamma t}{|\vec{r}_{\perp}|^2}$ and $w \equiv \frac{t}{|\vec{r}_{\perp}|^2}$. The asymptotic limits of G(u, w) and $C_v(\vec{r}, t)$ can be obtained by the following arguments.

When $r_{\parallel} - \gamma t \rightarrow 0$ and $t \rightarrow 0$, $C_v(\vec{r}, t)$ must clearly depend only on r_{\perp} , and should not vanish. Hence $G(u \ll 1, w \ll 1) \rightarrow \text{constant} \neq 0$. This in turn implies that $C_v(\vec{r}, t) \propto |\vec{r}_{\perp}|^{2\chi}$ for $|\vec{r}_{\perp}|^{\zeta} \gg |r_{\parallel} - \gamma t|$, $t^{\zeta/z}$. Similarly, if $\vec{r} \rightarrow 0$ and $t \rightarrow 0$, then $C_v(\vec{r}, t)$ should depend only on $|r_{\parallel} - \gamma t|$. This implies $G(u, w) \propto u^{2\chi/\zeta}$ for $u \gg w$, 1, in order to cancel off the $|\vec{r}_{\perp}|^{2\chi}$ prefactor in Eq. (20). This in turn implies that $C_v(\vec{r}, t) \propto |r_{\parallel} - \gamma t|^{2\chi/\zeta}$ for $|r_{\parallel} - \gamma t| \gg |\vec{r}_{\perp}|^{\zeta}$, $t^{\zeta/z}$. Similar reasoning implies that $C_v(\vec{r}, t) \propto |t|^{2\chi/z}$ for $t \gg |\vec{r}_{\perp}|^z$, $|r_{\parallel} - \gamma t|^{z/\zeta}$. Hence, using the exact exponents (1) in d = 2,

$$C_{\nu}(\vec{r},t) \propto \begin{cases} r_{\perp}^{-(2/5)}, & |r_{\perp}|^{3/5} \gg |r_{\parallel} - \gamma t|, t^{1/2} \\ (r_{\parallel} - \gamma t)^{-(2/3)}, & |r_{\parallel} - \gamma t| \gg |x|^{3/5}, t^{1/2} \\ t^{-(1/3)}, & |t| \gg |r_{\perp}|^{6/5}, |r_{\parallel} - \gamma t|^{2}. \end{cases}$$

$$(21)$$

This correlation function can be measured directly in both simulations [7,9], and experiments [14].

The relation (8) between density and velocity implies that density correlations should obey the same sort of scaling law, but with an additional power of $|r_{\perp}|^{-1}$ for every power of $\delta \rho$; hence, in d = 2:

$$C_{\rho}(\vec{r}, t) \equiv |r_{\perp}|^{-(12/5)} G_{\rho} \left(\frac{r_{\parallel} - \gamma t}{|r_{\perp}|^{3/5}}, \frac{t}{|r_{\perp}|^{6/5}} \right)$$

$$\propto \begin{cases} |r_{\perp}|^{-(12/5)}, & |r_{\perp}|^{3/5} \gg |r_{\parallel} - \gamma t|, t^{1/2} \\ (r_{\parallel} - \gamma t)^{-4}, & |r_{\parallel} - \gamma t| \gg |r_{\perp}|^{3/5}, t^{1/2} \\ t^{-2}, & |t| \gg |r_{\perp}|^{6/5}, |r_{\parallel} - \gamma t|^{2}. \end{cases}$$
(22)

The last line holds in d = 3 as well, because $\chi = 1 - z$ does. The last two lines of (22) directly imply Eqs. (3) and (4). It can also be shown [11] that at equal times $C_{\rho}(\vec{r}, t = 0)$ decays sufficiently rapidly that there are no giant number fluctuations in Malthusian flocks.

In conclusion, I have shown in this Letter that, as always in hydrodynamics, the removal of a conservation law (in the case I consider here, number conservation), leads to profound changes in the long-wavelength, long-time behavior of flocks. The sound modes of number conserving flocks disappear, and are replaced by drifting, hyperdiffusive modes. I have also shown that earlier claims that hydrodynamic scaling laws could be obtained for number conserving flocks are incorrect, but that it is possible to do so for number nonconserving, (Malthusian) flocks. In both Malthusian and immortal flocks, anomalous hydrodynamics stabilizes long-ranged orientational order (i.e., $\langle \vec{v}(\vec{r},t) \rangle \neq \vec{0}$ in spatial dimension d=2. In Malthusian flocks, the order outlives the boids: the persistence time diverges as the number of boids $N \rightarrow \infty$, while the lifetime of the boids remains finite in this limit. The theory presented here implies a number of experimentally observable consequences, including the anomalous persistence of number fluctuations in Malthusian flocks, which decay algebraically with time with universal power laws which are predicted herein.

I thank the Institut Poincare, the ESPCI, the Universite Pierre et Marie Curie, the KITP (UCSB), CUNY, the Lorentz Center, University of Leiden, and the MPI-PKS, Dresden, for their hospitality; S. Ramaswamy, H. Chate, A. Cavagna, I. Giardina, M. Rao, Y. Tu, and F. Ginelli for valuable discussions; and K. Toner for a careful reading of the manuscript. This work was supported by the National Science Foundation, Grant No. EF-1137815.

^[1] See, e.g., C. Reynolds, Computer Graphics Forum **21**, 25 (1987).

^[2] See, e.g., W. Loomis, *The Development of Dictyosteliumdiscoideum* (Academic, New York, 1982).

- [3] W.J. Rappel et al., Phys. Rev. Lett. 83, 1247 (1999).
- [4] R. Voituriez, J. F. Joanny, and J. Prost, Europhys. Lett. 70, 404 (2005).
- [5] K. Kruse, J.F. Joanny, F. Julicher, J. Prost, and K. Sekimoto, Eur. Phys. J. E 16, 5 (2005).
- [6] T. Vicsek et al., Phys. Rev. Lett. 75, 1226 (1995).
- [7] J. Toner and Y.-h. Tu, Phys. Rev. Lett. **75**, 4326 (1995);
 Y.-h. Tu, M. Ulm, and J. Toner, Phys. Rev. Lett. **80**, 4819 (1998);
 J. Toner and Y.-h. Tu, Phys. Rev. E **58**, 4828 (1998);
 J. Toner, Y.-h. Tu, and S. Ramaswamy, Ann. Phys. (N.Y.) **318**, 170 (2005).
- [8] N.D. Mermin and H. Wagner, Phys. Rev. Lett. 17, 1133 (1966); P.C. Hohenberg, Phys. Rev. 158, 383 (1967).
- [9] See, e.g., G. Gregoire, H. Chate, and Y.-h. Tu, Phys. Rev. Lett. 86, 556 (2001).
- [10] K. Gowrishankar, S. Ghosh, S. Saha, S. Mayor, and M. Rao (to be published).
- [11] J. Toner (to be published).
- [12] S. Mishra, R. A. Simha, and S. Ramaswamy, J. Stat. Mech. (2010) P02003 studied number nonconserving *apolar* flocks.

- [13] W. Mather *et al.*, Phys. Rev. Lett. **104**, 208101 (2010).
- [14] M. Ballerini *et al.*, Animal Behaviour **76**, 201 (2008).
- [15] The P_2 term was left out by all of Ref. [7], as was the density dependence of λ_1 . The latter oversight lead to the erroneous conclusion that one could determine exact exponents for immortal flocks in d = 2.
- [16] T. R. Malthus, An Essay on the Principle of Population, edited by J. Johnson (St. Paul's Churchyard, London, 1798).
- [17] This is an absolutely standard postulate of population dynamics; one commonly used model, namely $g(\rho) = \gamma \rho (1 \rho / \rho_0)$, where γ is the small density growth rate, is known as "logistical dynamics". See, e.g., M. A. Nowak, *Evolutionary Dynamics* (Belknap/Harvard University Press, Cambridge, Massachusetts, 2006).
- [18] See, e.g., D. Forster, D.R. Nelson, and M.J. Stephen, Phys. Rev. A 16, 732 (1977).