Hidden entropy production and work fluctuations in an ideal active gas

Suraj Shankar* and M. Cristina Marchetti[†]

Physics Department and Syracuse Soft and Living Matter Program, Syracuse University, Syracuse, New York 13244, USA and Kavli Institute for Theoretical Physics, University of California, Santa Barbara, California 93106, USA

(Received 15 April 2018; published 30 August 2018)

Collections of self-propelled particles that move persistently by continuously consuming free energy are a paradigmatic example of active matter. In these systems, unlike Brownian "hot colloids," the breakdown of detailed balance yields a continuous production of entropy at steady state, even for an ideal active gas. We quantify the irreversibility for a noninteracting active particle in two dimensions by treating both conjugated and time-reversed dynamics. By starting with underdamped dynamics, we identify a hidden rate of entropy production required to maintain persistence and prevent the rapidly relaxing momenta from thermalizing, even in the limit of very large friction. Additionally, comparing two popular models of self-propulsion with identical dissipation on average, we find that the fluctuations and large deviations in work done are markedly different, providing thermodynamic insight into the varying extents to which macroscopically similar active matter systems may depart from equilibrium.

DOI: 10.1103/PhysRevE.98.020604

Introduction. What is irreversible in active matter? These systems are driven out of equilibrium by the continuous and sustained consumption of free energy at the microscopic scale [1-3], but quantifying such irreversibility is challenging. The persistent motion of E. coli performing run and tumble [4,5] or of synthetic active colloids propelled by autophoresis [6,7] are classic examples of motion that breaks microscopic detailed balance by virtue of self-propulsion [8], yet is diffusive on large scales. The detailed balance violations due to persistence often do not survive coarse graining (even in the presence of weak external fields). This restores an effective equilibrium picture on large scales, thereby allowing a dilute gas of self-propelled particles to be essentially treated as a gas of "hot colloids" [9] with an effective temperature [10-13]. In characterizing detailed balance violations on a coarse-grained scale, even manifestly nonequilibrium phenomena, such as condensation in the absence of attraction [14,15], may then be understood by comparing them to the "nearest" equilibriumlike model at the same scale [16].

To quantify irreversibility of an ideal active gas, we examine here the microscopic dynamics of an individual active particle and evaluate the entropy production rate $\langle \Delta \dot{s} \rangle$ in two popular simple models of self-propelled particles in two dimensions (2D): Active Brownian particles (ABPs) where the propulsive force has fixed magnitude and its direction is randomized by rotational noise, and active Ornstein-Uhlenbeck particles (AOUPs) where self-propulsion is modeled as a Gaussian colored noise. Entropy production provides a direct measure of the breakdown of time-reversal symmetry (TRS) at steady state. We show below that it crucially hinges on whether the propulsive force is treated as even under TRS [17,18], appropriate for active phoretic colloids, vibrated rods, or swimming bacteria, where the direction of motility encodes a physical asymmetry of the microscopic active unit, or as odd under TRS [19-21], corresponding to the so-called conjugated dynamics [22]. Previous work has used both prescriptions, as well as techniques that leave the sign under TRS unspecified [23-26], all with differing and sometimes conflicting notions of dissipated heat and its relation to entropy production. Additionally, a single active particle has often been found to have vanishing entropy production [21,23–26], seemingly suggesting equilibrium behavior. We show that some of these issues can be clarified by using underdamped dynamics along with thermal noise and taking the large friction limit only at the end, because for both TRS prescriptions the fast momenta degrees of freedom are responsible for a finite hidden entropy production [27-30], thereby demonstrating that a single active particle is thermodynamically irreversible. This is most evident for the case of conjugated dynamics where the hidden $\langle \Delta \dot{s} \rangle$ is the only contribution, while it is subdominant at large friction for TRS-even propulsive forces (see Table I). If, in contrast, inertia is neglected from the outset, a single active particle behaves as a passive colloid pulled by an external force (TRS-even propulsion) or as a colloid moving at the velocity of the solvent in a sheared fluid [21,31] (propulsion here is the solvent velocity, which is TRS odd), with $\langle \Delta \dot{s} \rangle = 0$. This result holds for both ABP and AOUP, thereby not distinguishing the two models on the average.

We then show that the nonequilibrium nature of active particles becomes evident in the *fluctuations* of thermodynamic quantities. By comparing the ABP and the AOUP models, we find that even though they have the same long-time dynamics and dissipate identically on average, their work fluctuations are vastly different. We demonstrate in a precise fashion that the AOUP gas is always further away from equilibrium compared to the ABP gas, for the same motility and persistence. Specifically, the variance of the cumulative work done to propel

^{*}sushanka@syr.edu

[†]Current address: Department of Physics, University of California, Santa Barbara, CA 93106; mcmarche@syr.edu

TABLE I. A summary of the average entropy production rate $\langle \Delta s \rangle$ for various cases, applicable to both noninteracting ABP and AOUP (using $T_a = v_0^2 \gamma / 2D_R$). The difference between the results obtained with underdamped and overdamped dynamics represents the hidden entropy production.

$\overline{\langle \Delta \dot{s} \rangle}$	Overdamped	Underdamped
TRS-odd propulsion	0	$\frac{v_0^2 \gamma D_R}{T(\gamma + D_R)}$
TRS-even propulsion	$\frac{v_0^2\gamma}{T}$	$\frac{\frac{v_0^2 \gamma^2}{T(\gamma + D_R)}}{T(\gamma + D_R)}$

the particles, corresponding to the Fano factor, is strongly enhanced by activity over its linear response value for the AOUP, but not for the ABP. Our work can be extended to thermodynamic quantities of interacting active systems along with their fluctuations that are beginning to be accessible experimentally [32–36].

The models. We consider an underdamped active particle and set the mass and Boltzmann factor to unity. The particle velocity $\dot{\mathbf{r}} = \mathbf{p}$ obeys a Langevin equation,

$$\dot{\mathbf{p}} = -\gamma \mathbf{p} + \mathbf{f}_p + \sqrt{2T\gamma} \,\boldsymbol{\xi}(t), \tag{1}$$

where γ is the friction, T the temperature of the environment providing a heat bath, and $\xi(t)$ a delta-correlated Gaussian white noise. For ABP the propulsive force $\mathbf{f}_p = \gamma v_0 \hat{\mathbf{e}}$ has fixed magnitude, with v_0 the self-propulsion speed, and direction randomized by rotational noise, $\langle \hat{\mathbf{e}}(t) \cdot \hat{\mathbf{e}}(0) \rangle = e^{-|t|D_R}$. For AOUP the propulsive force is an Ornstein-Uhlenbeck process, $D_R^{-1} \dot{\mathbf{f}}_p = -\mathbf{f}_p + \sqrt{2\gamma T_a} \boldsymbol{\eta}(t) [\boldsymbol{\eta}(t)]$ white noise and T_a an active temperature], so that $\langle \mathbf{f}_p(t) \cdot \mathbf{f}_p(0) \rangle = 2\gamma T_a D_R e^{-|t|D_R}$. Both types of particles are diffusive at long times, with diffusivity $D = (T + T_a)/\gamma$, where for ABP, $T_a = v_0^2 \gamma/(2D_R)$. It has been shown that the large-scale phenomenology of the two models is similar even in the presence of strong interactions [37,38] where they both exhibit motility-induced phase separation. Yet, as we shall show below, their thermodynamic fluctuations are markedly different even at the single particle level.

Mean entropy production. Irreversibility can be quantified through dissipation and entropy production, which can be calculated within the framework of stochastic thermodynamics [22]. At steady state, the total entropy production of the system equals the entropy flux to the environment (also called entropy production of the medium [39]). For a time interval [0, t], it is given by [40]

$$\Delta s(t) = \ln\left(\frac{P[\mathbf{x}(t)|\mathbf{x}(0)]}{P^{\dagger}[\mathbf{x}^{\dagger}(t)|\mathbf{x}^{\dagger}(0)]}\right),\tag{2}$$

where $\mathbf{x} = {\mathbf{r}, \mathbf{p}, \mathbf{f}_p}$ and $P[\mathbf{x}(t)|\mathbf{x}(0)]$ is the conditional probability of starting at $\mathbf{x}(0)$ at time $\tau = 0$ and reaching $\mathbf{x}(t)$ at time $\tau = t$ along a given trajectory $\mathbf{x}(\tau)$. The \dagger denotes time reversal. The conditional probability for observing a forward trajectory $\mathbf{x}(\tau)$ ($\tau \in [0, t]$) is formally written as $P[\mathbf{x}(t)|\mathbf{x}(0)] \propto e^{-\mathcal{A}} \prod_{\tau=0}^t \delta(\partial_{\tau}\mathbf{r} - \mathbf{p})$, where $\mathcal{A}[\mathbf{x}(\tau)]$ is the Onsager-Machlup functional [41] (neglecting unimportant additive constants [42]), given by

$$\mathcal{A} = \frac{1}{4T\gamma} \int_0^t d\tau [\partial_\tau \mathbf{p} + \gamma \mathbf{p} - \mathbf{f}_p]^2.$$
(3)

For noninteracting particles, the Hamiltonian of the system only involves the kinetic energy ($\mathcal{H} = \mathbf{p}^2/2$) and the first law takes the form (in Stratanovich convention) [43]

$$d\mathcal{H} = \mathbf{p} \cdot d\mathbf{p} = dw - dq, \qquad (4)$$

where dw is the propulsive work done and dq is the heat dissipated into the reservoir. The sign convention used is that both heat dissipated into the bath and work done by the environment on the system are taken to be positive. Requiring the Clausius relation, we equate $dq(t) = T\Delta s(t)$, which as we will see below is consistent with Sekimoto's [43] definition of heat only for the TRS-even case. It is clear from Eq. (2) that, as discussed in the Introduction, entropy production depends on whether the propulsion is treated as a force (hence TRS even) or as a velocity (hence TRS odd). We discuss both cases here, although the TRS-even prescription is more directly relevant to physical realizations. Also, the calculation of the mean entropy production is outlined here for ABP. The result turns out to be the same for AOUP.

TRS-odd propulsion. The prescription of conjugated dynamics $[\mathbf{r}^{\dagger}(\tau) = \mathbf{r}(t - \tau), \mathbf{p}^{\dagger}(\tau) = -\mathbf{p}(t - \tau), \text{ and } \mathbf{f}_{p}^{\dagger}(\tau) = -\mathbf{f}_{p}(t - \tau)$ on a time interval $\tau \in [0, t]$; see Fig. 1(a)] most clearly illustrates the importance of retaining the fast momenta degrees of freedom and the associated hidden entropy production. Considering from the outset overdamped dynamics and treating motility as a TRS-odd velocity seems to lead identically to $\Delta \dot{s} = 0$, in the absence of interactions [21,23], wrongly suggesting that the system is in equilibrium [44]. Working instead with the underdamped equations, we obtain the entropy production rate to be $\Delta \dot{s} = -\dot{\mathbf{p}} \cdot (\mathbf{p} - v_0 \hat{\mathbf{e}})/T$. Averaging over noise, in steady state, we get

$$\langle \Delta \dot{s} \rangle = \frac{v_0^2 \gamma D_R}{T(\gamma + D_R)} = \frac{v_0^2}{T} D_R + O\left(\frac{D_R}{\gamma}\right).$$
(5)

This demonstrates a hidden entropy production in active matter arising from the entropic cost to maintain a finite persistence and evade thermalization of the fast momentum. By taking the overdamped limit at the very outset, i.e., $t \gg \gamma^{-1}$, the momentum is implicitly assumed to have relaxed to the equilibrium Maxwell-Boltzmann distribution, but this is simply not true on timescales of $O(D_R^{-1})$ due to the persistence of motion. As the momentum of the active particle is effectively slaved to the motility, on short timescales $(\sim \gamma^{-1})$ it relaxes to the stationary nonequilibrium distribution $P_{ss}(\mathbf{p}|\hat{\mathbf{e}}) \propto \exp(-|\mathbf{p}-v_0\hat{\mathbf{e}}|^2/2T)$ [45]. On timescales $\sim D_R^{-1}(>\gamma^{-1})$, the polarization direction decorrelates, but it also forces the momentum to do the same in tandem, an act that requires work to be done and dissipated irreversibly. For $\gamma/D_R \gg 1$, one can also view $\langle \Delta \dot{s} \rangle$ as the symmetrized relative entropy (or the symmetrized Kullback-Leibler divergence [46]),

$$\Delta s_{\rm rel} = -\int \frac{d\hat{\mathbf{e}}}{2\pi} \int d^2 p [P_{\rm eq}(\mathbf{p}) - P_{ss}(\mathbf{p}|\hat{\mathbf{e}})] \ln\left(\frac{P_{ss}(\mathbf{p}|\hat{\mathbf{e}})}{P_{\rm eq}(\mathbf{p})}\right),\tag{6}$$

dissipated to the bath in a rotational correlation time D_R^{-1} , with $P_{\rm eq}(\mathbf{p}) \propto \exp(-p^2/2T)$. For $D_R = 0$, the system behaves as if it were in a background steady deterministic flow and $\langle \Delta \dot{s} \rangle$ vanishes.



FIG. 1. A cartoon of the trajectories under (a) time conjugated dynamics (\mathbf{f}_p is TRS odd) and (b) time-reversed dynamics (\mathbf{f}_p is TRS even) for a polar self-propelled particle.

TRS-even propulsion. If motility is treated as a TRS-even *nonconservative force* [Fig. 1(b)], a single active particle is then analogous to a driven colloid. In this case **r** and **p** transform as before under time reversal, but $\mathbf{f}_p^{\dagger}(\tau) = \mathbf{f}_p(t - \tau)$. Using Eqs. (3) and (2), the entropy production rate is identified as $\Delta \dot{s} = \mathbf{p} \cdot (\gamma \mathbf{p} - \sqrt{2T\gamma} \boldsymbol{\xi})/T$. The rate of heat dissipated $\dot{q} = T \Delta \dot{s}$ is as expected with $\mathbf{p} = \dot{\mathbf{r}}$ [43] and the rate of work done [from Eq. (4)] is given by $\dot{w} = v_0 \gamma \hat{\mathbf{e}} \cdot \mathbf{p}$, which is the power injected by the propulsive force \mathbf{f}_p . At steady state, the average rate of dissipation is

$$\langle \dot{q} \rangle = \langle \dot{w} \rangle = \frac{v_0^2 \gamma^2}{\gamma + D_R} \simeq v_0^2 \gamma \left[1 + O\left(\frac{D_R}{\gamma}\right) \right].$$
 (7)

For $\gamma \gg D_R$ the mean dissipation rate is the same as for a particle dragged by a constant force $v_0\gamma$. Starting from the outset with overdamped equations yields identically $\langle \dot{q} \rangle = \langle \dot{w} \rangle = v_0^2 \gamma$. Therefore when self-propulsion is treated as a TRS-even force, all hidden entropy contributions only appear at subleading order in D_R/γ .

The mean entropy production rate for the various combinations considered here is summarized in Table I [47]. Identifying $T_a = v_0^2 \gamma / 2D_R$ relates the AOUP model to the ABP, highlighting that both models have the same mean dissipation rate at steady state. So, the two models are thermodynamically identical *on average*.

Work fluctuations. The difference between the two models and true nonequilibrium nature becomes apparent in their *fluctuations.* We compute the variance of the cumulative work $\Delta w(t) = \int_0^t d\tau \, \dot{w}(\tau)$ done in propelling the active particle for a time *t*. Here, we consider only the physically relevant TRS-even case. At long times $(t \to \infty)$, we have

$$\langle \Delta w(t)^2 \rangle - \langle \Delta w(t) \rangle^2 = 2T_w \langle \Delta w(t) \rangle, \tag{8}$$

where T_w (the Fano factor) is an effective temperature for work fluctuations (distinct from the active temperature T_a). One can compute T_w through a Green-Kubo-like formula, relating it to the time autocorrelation of the power input,

$$T_w = \frac{1}{\langle \dot{w} \rangle} \int_0^\infty dt [\langle \dot{w}(t) \dot{w}(0) \rangle - \langle \dot{w} \rangle^2].$$
(9)

As T_w quantifies the relative fluctuations of \dot{w} , a current, it obeys a universal bound at steady state, $T_w \ge T$, first conjectured for out-of equilibrium reaction networks [48] and later proven in a general stronger form by Gingrich *et al.* [49]. A remarkable result, the universal bound provides an uncertainty relation between current fluctuations and dissipation, generalizing equilibrium fluctuation-dissipation theorems [50] to far from equilibrium steady states.

For the underdamped ABP we find

$$T_w^{\text{ABP}} = T + \frac{\langle \dot{w} \rangle D_R^2}{\gamma(\gamma + D_R)(\gamma + 2D_R)} \simeq T, \qquad (10)$$

where the second equality holds for negligible inertia $(\gamma/D_R \rightarrow \infty)$, i.e., the ABP *saturates* the universal dissipation bound $(T_w = T)$ for *arbitrary* motility and persistence. An important and surprising consequence of this result is that a free overdamped ABP gas is *always* within the *linear* response regime from a steady state with detailed balance, regardless of what v_0 or D_R are. This is especially counterintuitive given that for large v_0 the velocity distribution is non-Maxwellian and bimodal [Fig. 2(a)]. Since the particle is linearly close to equilibrium, all higher cumulants of the work done vanish and one can easily compute the large deviation functional for the work current J_t , at steady state for large friction, with the result [see Figs. 3(a) and 3(b)]

$$\lim_{t \to \infty} -\frac{1}{t} \ln P\left(\frac{\Delta w(t)}{t} = J_t\right) = \frac{(J_t - \langle \dot{w} \rangle)^2}{4T \langle \dot{w} \rangle}.$$
 (11)

In other words, the work distribution is Gaussian and satisfies a fluctuation theorem $\langle e^{-\Delta w/T} \rangle = 1$ [22,39]. In Ref. [51], it was shown that overdamped 2*d* chiral active Brownian particles also similarly saturate the dissipation bound and are hence linearly close to equilibrium as well.



FIG. 2. The steady state probability distribution of the particle momentum is plotted for (a) the ABP model with $v_0 = 1$ (blue) and $v_0 = 10$ (red), and (b) the AOUP model with $v_0 = 1$ (blue) and $v_0 = 10$ (red). As both p_x and p_y are identically distributed, they are plotted with the same color and symbol. Parameters $\gamma = 100$, $D_R = 1$, and T = 1 are chosen common.



FIG. 3. The large deviation function of work done in the ABP [(a) $v_0 = 1$, (b) $v_0 = 10$] and AOUP [(c) $v_0 = 1$, (d) $v_0 = 10$] models. The black lines in all four plots are the theoretical predictions from Eqs. (11) and (13) for the two models. The other parameters are $\gamma = 100$, $D_R = 1$, and T = 1.

Doing the same, we compute the work fluctuations for the AOUP, with the result

$$T_w^{\text{AOUP}} = T + T_a + \frac{\langle \dot{w} \rangle}{2(D_R + \gamma)}.$$
 (12)

Unlike the ABP, the AOUP model *does not* saturate the universal bound on dissipation in the limit of large friction. In fact, $T_w^{\text{AOUP}} \simeq T + T_a$ (for $\gamma \gg D_R$) [52], indicating that the system moves further way from the equilibrium steady state (and the linear response regime) with increasing active temperature T_a . These enhanced work fluctuations arise from the fact that the fluctuations of the propulsive force \mathbf{f}_p are unbounded for AOUP and lead to the power input being correlated on longer timescales $\sim D_R^{-1}$ [instead of $(\gamma + D_R)^{-1}$ as for the ABP model]. Our results suggest that tracers in an active bath that are usually thought to be well described as AOUP [53] may be thermodynamically distinct from actual active particles.

One can also compute the large-deviation function of work done, for the AOUP model (see Ref. [54] for the derivation). We compute the cumulant generating function $\mathcal{F}(\lambda) =$ $-\ln \langle e^{-\lambda \Delta w(t)} \rangle / t$ as an eigenvalue of a tilted Fokker-Planck operator [40] using a Gaussian ansatz for the corresponding eigenfunction, with the result

$$\frac{\mathcal{F}(\lambda)}{\gamma} = -1 - \frac{D_R}{\gamma} + \sqrt{1 + \frac{D_R^2}{\gamma^2} + 2\frac{D_R}{\gamma}\sqrt{1 + 4T_a\lambda(1 - T\lambda)}}.$$
(13)

This function has branch cuts outside the interval $[\lambda_{-}, \lambda_{+}]$,

- S. Ramaswamy, The mechanics and statistics of active matter, Annu. Rev. Condens. Matter Phys. 1, 323 (2010).
- [2] M. C. Marchetti, J.-F. Joanny, S. Ramaswamy, T. B. Liverpool, J. Prost, M. Rao, and R. Aditi Simha, Hydrodynamics

with $\lambda_{\pm} = [1 \pm \sqrt{1 + T/T_a}]/(2T)$ leading to exponential non-Gaussian tails in the work distribution. The large-deviation function is then obtained by a Legendre transform of $\mathcal{F}(\lambda)$ and is shown in Figs. 3(c) and 3(d). A Gallavotti-Cohen-like symmetry [40] is realized here as $\mathcal{F}(\lambda) = \mathcal{F}(T^{-1} - \lambda)$ and leads to a corresponding detailed fluctuation theorem for $P(\Delta w)$. Extreme rare fluctuations in the AOUP model are far in excess than in the ABP. As recent experiments have measured both Gaussian and non-Gaussian large deviations in a self-propelled particle [32], we expect our results can advise the thermodynamically appropriate modeling of such particles. It would be interesting to see how these fluctuations change when interactions are added in both models and how these results will play out when extended to coarse-grained scales. Some recent works [55,56] have correlated large deviations in work to clustering and phase separation in interacting active systems. Even from our single particle treatment, we see that large fluctuations are controlled by the statistics of persistence (that can be modified by interactions) and encodes the time correlation of the power input $\langle \dot{w}(t)\dot{w}(0)\rangle$. A comparison including the interaction time scale in the power autocorrelation is left for future work.

Conclusions. To conclude, we have argued the importance of including fast degrees of freedom in thermodynamic treatments of active matter and shown how one may gain different notions of irreversibility from conjugated and time-reversed dynamics. The presence of hidden entropy production extends to other situations as well, for example, in chiral active rotors [57,58] one would have to retain the fast angular momentum as well. Additionally, in cases where self-propulsion ultimately comes from an underlying microscopic chemical reaction, the chemical variable must be retained to obtain the physical dissipation experimentally measurable in the system. By working within a Langevin framework as in Ref. [3] we correctly reproduce [54] the recent results of Pietzonka and Seifert[18], without having to introduce a discrete lattice model. The claimed failure of the time-reversal procedure at the level of stochastic trajectories [18] is then seen to be a consequence of the hidden entropy production. Finally, we emphasize the importance of going beyond average quantities and look at fluctuations of the work done in propelling two model active systems. Comparing the ABP and the AOUP models, we find that even though they have the same long-time dynamics and dissipate identically on average, their work fluctuations are vastly different, signaling their distinct nonequilibrium features.

Acknowledgments. We thank Sriram Ramaswamy for helpful discussions and Andrea Puglisi for useful comments. This work was primarily supported by NSF-DMR-1609208. Additional support was provided by NSF-DGE-1068780 (M.C.M.) and by NSF-PHY-1748958 (S.S., M.C.M.). The authors also acknowledge support of the Syracuse University Soft and Living Matter Program and thank the KITP for hospitality during part of this project.

of soft active matter, Rev. Mod. Phys. **85**, 1143 (2013).

^[3] S. Ramaswamy, Active matter, J. Stat. Mech.: Theor. Exp. (2017) 054002.

- [4] M. J. Schnitzer, Theory of continuum random walks and application to chemotaxis, Phys. Rev. E 48, 2553 (1993).
- [5] H. C. Berg, E. coli in Motion (Springer, Berlin, 2008).
- [6] W. F. Paxton, S. Sundararajan, T. E. Mallouk, and A. Sen, Chemical locomotion, Angew. Chem., Int. Ed. 45, 5420 (2006).
- [7] J. R. Howse, R. A. L. Jones, A. J. Ryan, T. Gough, R. Vafabakhsh, and R. Golestanian, Self-Motile Colloidal Particles: From Directed Propulsion to Random Walk, Phys. Rev. Lett. 99, 048102 (2007).
- [8] M. E. Cates, Diffusive transport without detailed balance in motile bacteria: Does microbiology need statistical physics? Rep. Prog. Phys. 75, 042601 (2012).
- [9] J. Tailleur and M. E. Cates, Sedimentation, trapping, and rectification of dilute bacteria, Europhys. Lett. 86, 60002 (2009).
- [10] D. Loi, S. Mossa, and L. F. Cugliandolo, Effective temperature of active matter, Phys. Rev. E 77, 051111 (2008).
- [11] J. Palacci, C. Cottin-Bizonne, C. Ybert, and L. Bocquet, Sedimentation and Effective Temperature of Active Colloidal Suspensions, Phys. Rev. Lett. 105, 088304 (2010).
- [12] G. Szamel, Self-propelled particle in an external potential: Existence of an effective temperature, Phys. Rev. E 90, 012111 (2014).
- [13] F. Ginot, I. Theurkauff, D. Levis, C. Ybert, L. Bocquet, L. Berthier, and C. Cottin-Bizonne, Nonequilibrium Equation of State in Suspensions of Active Colloids, Phys. Rev. X 5, 011004 (2015).
- [14] J. Tailleur and M. E. Cates, Statistical Mechanics of Interacting Run-and-Tumble Bacteria, Phys. Rev. Lett. 100, 218103 (2008).
- [15] M. E. Cates and J. Tailleur, Motility-induced phase separation, Annu. Rev. Condens. Matter Phys. 6, 219 (2015).
- [16] C. Nardini, É. Fodor, E. Tjhung, F. van Wijland, J. Tailleur, and M. E. Cates, Entropy Production in Field Theories without Time-Reversal Symmetry: Quantifying the Nonequilibrium Character of Active Matter, Phys. Rev. X 7, 021007 (2017).
- [17] T. Speck, Stochastic thermodynamics for active matter, Europhys. Lett. 114, 30006 (2016).
- [18] P. Pietzonka and U. Seifert, Entropy production of active particles and for particles in active baths, J. Phys. A: Math. Theor. 51, 01LT01 (2017).
- [19] C. Ganguly and D. Chaudhuri, Stochastic thermodynamics of active Brownian particles, Phys. Rev. E 88, 032102 (2013).
- [20] D. Chaudhuri, Active Brownian particles: Entropy production and fluctuation response, Phys. Rev. E 90, 022131 (2014).
- [21] T. Speck, Geometric view of stochastic thermodynamics for nonequilibrium steady states, arXiv:1707.05289.
- [22] U. Seifert, Stochastic thermodynamics, fluctuation theorems and molecular machines, Rep. Prog. Phys. 75, 126001 (2012).
- [23] É. Fodor, C. Nardini, M. E. Cates, J. Tailleur, P. Visco, and F. van Wijland, How Far from Equilibrium is Active Matter? Phys. Rev. Lett. 117, 038103 (2016).
- [24] U. M. B. Marconi, A. Puglisi, and C. Maggi, Heat, temperature and clausius inequality in a model for active Brownian particles, Sci. Rep. 7, 46496 (2017).
- [25] D. Mandal, K. Klymko, and M. R. DeWeese, Entropy Production and Fluctuation Theorems for Active Matter, Phys. Rev. Lett. 119, 258001 (2017).
- [26] A. Puglisi and U. M. B. Marconi, Clausius relation for active particles: What can we learn from fluctuations, Entropy 19, 356 (2017).

- [27] A. Celani, S. Bo, R. Eichhorn, and E. Aurell, Anomalous Thermodynamics at the Microscale, Phys. Rev. Lett. 109, 260603 (2012).
- [28] K. Kawaguchi and Y. Nakayama, Fluctuation theorem for hidden entropy production, Phys. Rev. E 88, 022147 (2013).
- [29] H.-M. Chun and J. D. Noh, Hidden entropy production by fast variables, Phys. Rev. E 91, 052128 (2015).
- [30] M. Esposito, Stochastic thermodynamics under coarse graining, Phys. Rev. E 85, 041125 (2012).
- [31] T. Speck, J. Mehl, and U. Seifert, Role of External Flow and Frame Invariance in Stochastic Thermodynamics, Phys. Rev. Lett. 100, 178302 (2008).
- [32] N. Kumar, S. Ramaswamy, and A. K. Sood, Symmetry Properties of the Large-Deviation Function of the Velocity of a Self-Propelled Polar Particle, Phys. Rev. Lett. **106**, 118001 (2011).
- [33] A. Argun, A.-R. Moradi, E. Pinçe, G. B. Bagci, A. Imparato, and G. Volpe, Non-Boltzmann stationary distributions and nonequilibrium relations in active baths, Phys. Rev. E 94, 062150 (2016).
- [34] N. Kumar, H. Soni, S. Ramaswamy, and A. K. Sood, Anisotropic isometric fluctuation relations in experiment and theory on a self-propelled rod, Phys. Rev. E 91, 030102(R) (2015).
- [35] C. Battle, C. P. Broedersz, N. Fakhri, V. F. Geyer, J. Howard, C. F. Schmidt, and F. C. MacKintosh, Broken detailed balance at mesoscopic scales in active biological systems, Science 352, 604 (2016).
- [36] É. Fodor, W. W. Ahmed, M. Almonacid, M. Bussonnier, N. S. Gov, M.-H. Verlhac, T. Betz, P. Visco, and F. van Wijland, Nonequilibrium dissipation in living oocytes, Europhys. Lett. 116, 30008 (2016).
- [37] Y. Fily and M. C. Marchetti, Athermal Phase Separation of Self-Propelled Particles with No Alignment, Phys. Rev. Lett. 108, 235702 (2012).
- [38] T. F. F. Farage, P. Krinninger, and J. M. Brader, Effective interactions in active Brownian suspensions, Phys. Rev. E 91, 042310 (2015).
- [39] U. Seifert, Entropy Production Along a Stochastic Trajectory and an Integral Fluctuation Theorem, Phys. Rev. Lett. 95, 040602 (2005).
- [40] J. L. Lebowitz and H. Spohn, A Gallavotti-Cohen-type symmetry in the large deviation functional for stochastic dynamics, J. Stat. Phys. 95, 333 (1999).
- [41] L. Onsager and S. Machlup, Fluctuations and irreversible processes, Phys. Rev. 91, 1505 (1953).
- [42] The dynamics of \mathbf{f}_p in both models also contribute terms to \mathcal{A} but are not consequential for our present discussion. In the AOUP model, this leads to an additional rate of entropy production $\Delta \dot{s}_R = \mathbf{f}_p \cdot [\mathbf{f}_p \sqrt{2\gamma T_a} \boldsymbol{\eta}(t)]/(\gamma T_a)$, absent in the ABP model. At steady state, $\langle \Delta \dot{s}_R \rangle = 0$ and it decouples from the rest of the dynamics, so we do not consider it any further.
- [43] K. Sekimoto, Langevin equation and thermodynamics, Prog. Theor. Phys. Suppl. 130, 17 (1998).
- [44] Note that the procedure of Refs. [23–25] cannot be used in the presence of translational noise with $T \neq 0$.
- [45] A. Baskaran and M. C. Marchetti, Nonequilibrium statistical mechanics of self-propelled hard rods, J. Stat. Mech.: Theor. Exp. (2010) P04019.
- [46] S. Kullback and R. A. Leibler, On information and sufficiency, Ann. Math. Statist. 22, 79 (1951).

- [47] These results can easily be extended to anisotropic friction $\boldsymbol{\gamma} = \gamma_{||} \hat{\mathbf{e}} \hat{\mathbf{e}} + \gamma_{\perp} (\mathbf{1} \hat{\mathbf{e}} \hat{\mathbf{e}})$, where, for example, the average dissipation rate for a TRS-even propulsion is $\langle \dot{q} \rangle = v_0^2 \gamma_{||}^2 / (\gamma_{||} + D_R)$.
- [48] A. C. Barato and U. Seifert, Thermodynamic Uncertainty Relation for Biomolecular Processes, Phys. Rev. Lett. 114, 158101 (2015).
- [49] T. R. Gingrich, J. M. Horowitz, N. Perunov, and J. L. England, Dissipation Bounds All Steady-State Current Fluctuations, Phys. Rev. Lett. 116, 120601 (2016).
- [50] R. Kubo, The fluctuation-dissipation theorem, Rep. Prog. Phys. 29, 255 (1966).
- [51] S. Pigolotti, I. Neri, É. Roldán, and F. Jülicher, Generic Properties of Stochastic Entropy Production, Phys. Rev. Lett. 119, 140604 (2017).
- [52] Here, we take the large friction limit at fixed T_a . Keeping a putative self-propulsion speed $v_0 = \sqrt{2T_a D_R/\gamma}$ fixed instead only results in a higher T_w^{AOUP} .

- [53] C. Maggi, M. Paoluzzi, N. Pellicciotta, A. Lepore, L. Angelani, and R. Di Leonardo, Generalized Energy Equipartition in Harmonic Oscillators Driven by Active Baths, Phys. Rev. Lett. 113, 238303 (2014).
- [54] See Supplemental Material at http://link.aps.org/supplemental/ 10.1103/PhysRevE.98.020604 for a derivation.
- [55] F. Cagnetta, F. Corberi, G. Gonnella, and A. Suma, Large Fluctuations and Dynamic Phase Transition in a System of Self-Propelled Particles, Phys. Rev. Lett. 119, 158002 (2017).
- [56] S. Whitelam, K. Klymko, and D. Mandal, Phase separation and large deviations of lattice active matter, J. Chem. Phys. 148, 154902 (2018).
- [57] P. Lenz, J.-F. Joanny, F. Jülicher, and J. Prost, Membranes with Rotating Motors, Phys. Rev. Lett. 91, 108104 (2003).
- [58] B. C. van Zuiden, J. Paulose, W. T. M. Irvine, D. Bartolo, and V. Vitelli, Spatiotemporal order and emergent edge currents in active spinner materials, Proc. Natl. Acad. Sci. USA 113, 12919 (2016).