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Flow interactions lead to orderly formations of flapping wings in forward flight

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Classic models of fish schools and flying formations of birds are built on the hypothesis that the preferred locations of an individual are determined by the flow left by its upstream neighbor. Lighthill posited that arrangements may in fact emerge passively from hydro- or aerodynamic interactions, drawing an analogy to the formation of crystals by intermolecular forces. Here, we carry out physical experiments aimed at testing the Lighthill conjecture and find that self-propelled flapping wings spontaneously assume one of multiple arrangements due to flow interactions. Wings in a tandem pair select the same forward speed, which tends to be faster than a single wing, while maintaining a separation distance that is an integer multiple of the wavelength traced out by each body. When perturbed, these locomotors robustly return to the same arrangement, and direct hydrodynamic force measurements reveal springlike restoring forces that maintain group cohesion. We also use these data to construct an interaction potential, showing how the observed positions of the follower correspond to stable wells in an energy landscape. Flow visualization and vortex-based theoretical models reveal coherent interactions in which the follower surfs on the periodic wake left by the leader. These results indicate that, for the high-Reynolds-number flows characteristic of schools and flocks, collective locomotion at enhanced speed and in orderly formations can emerge from flow interactions alone. If true for larger groups, then the view of collectives as ordered states of matter may prove to be a useful analogy.

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The interaction of many bodies through a fluid occurs in many natural and industrial contexts and often leads to surprising behaviors, such as correlated motions over long length scales [1,2]. Of particular interest are collections of actively propelled bodies, in which case each object induces flows during locomotion and also responds to flows generated by others. Biological examples include suspensions of swimming bacteria [3], insect swarms [4], krill swarms [5], fish schools [6], and bird flocks [7]. From an engineering perspective, such systems represent many-body fluid-structure interactions, and our understanding of these could lead to applications such as novel materials composed of active microparticles [8], arrangements of propulsors for air or water vehicles [9], and devices that harvest energy from flows [10]. From a physics perspective, collectively locomoting ensembles have been viewed as states of active matter [11], and to date efforts have focused on low-Reynolds-number systems in which the dynamics of microscopic constituents are coupled through viscous flows [12]. Less is known about interactions among large and fast-moving bodies, where inertial effects lead to jets, vortices, and other unsteady and spatially complex flows.

Animal schools and flocks are archetypes of such high-Reynolds-number collective locomotion, and fluid dynamical studies have focused on the role of flows in setting group structure and imparting collective advantages such as energetic savings [7,13]. Classic models of ordered groups are based on the idea that each individual adopts a preferred location that leads to constructive interactions with the wavelike or spatially periodic flow left by its upstream neighbor or neighbors [6,14].

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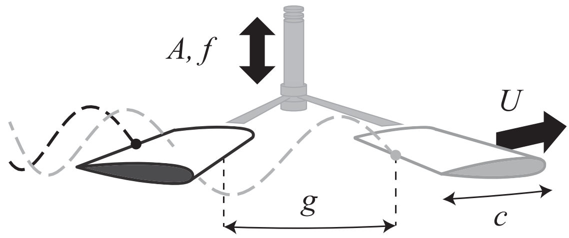

FIG. 1. Interacting and freely swimming flapping wings. A pair of wings or hydrofoils of chord length c are driven to undergo up-and-down heaving motions of peak-to-peak amplitude A and frequency f. The vertical motion is imposed by a motor (not shown) that drives the upright axle to which each wing is connected via a support rod and rotary bearing. The resulting forward locomotion takes the form of rotational orbits within a water tank, and the emergent swimming speed U and separation gap g are measured.

Extension of this few-body interaction across all members leads to a crystalline pattern, such as a V formation of evenly spaced birds [14] or a diamond-shaped lattice of fish [6]. In the 1970s, the applied mathematician and fluid dynamicist Sir James Lighthill proposed that, for sufficiently fast locomotion and thus strong flows, orderly patterns could arise passively from aero- or hydrodynamic interactions, without the need for collective decision making or active control mechanisms [15]. This hypothesis of flow-induced formation locomotion, which we call the *Lighthill conjecture*, seems to have not been experimentally tested or observed.

Physical experiments provide a promising means toward addressing this conjecture and for better understanding high-Reynolds-number interactions generally, and the two-body problem is a natural starting point. This approach has been used to study the hydrodynamic coupling between passively flapping bodies in a flow [16] as well as actively flapping wings or hydrofoils [17–20]. Studies of tandem wings held at fixed separation and immersed in an imposed flow show that the force generated by a follower depends on its interaction with vortices shed by its upstream neighbor [17,19,21,22]. To address the Lighthill conjecture, however, requires setting the bodies free to interactively select their speed and relative position, and recent studies have taken steps toward realizing the emergent locomotion dynamics. For example, experiments show that arrays of flapping and self-propelled wings select one of two speeds due to coherent flow-mediated interactions [23], though the spacing between bodies was fixed so the formation was imposed in that work. Intriguingly, recent computational fluid dynamics simulations show that two flapping, flexible, and freely spacing filaments adopt discrete separation distances during swimming [24].

Inspired by these works, here we aim to realize an experimental system to investigate the Lighthill conjecture, to assess emergent configurations and potential benefits from formations, and to provide insight into the underlying fluid dynamical mechanisms. We study a simple system composed of tandem wings flapping in synchrony, and understanding this two-body problem could provide insights into larger collectives. Importantly, these bodies are free to select both their speed and separation distance, and thus the observed dynamics and configurations serve as signatures of their flow-mediated coupling.

Experimental approach. As shown in the schematic of Fig. 1, wings or hydrofoils are driven to flap with the same up-and-down motion in water. Once flapped, the wings move forward as a result of the interaction with the fluid [25,26] and approach a terminal swimming speed over about ten flapping periods. Here we highlight key features of the setup, and additional details and video (Movie S1) are available as Supplemental Material [27]. A motor drives oscillations of a vertical axle to which each wing is attached via a separate support rod and independent sets of rotary bearings. The up-and-down heaving motion is thus prescribed but each wing is free to move in the direction transverse to flapping. The swimming motion is constrained to orbits around a water tank, and this rotational system reproduces key aspects of translational locomotion while allowing for long travel distances [23,25,26,28,29]. The peak-to-peak amplitude A and frequency f of the heaving motion

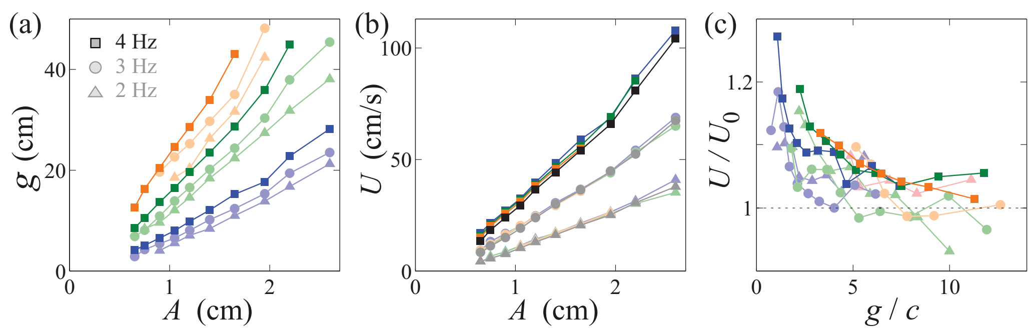

FIG. 2. Emergent spacing and speed. (a) Measured gap for motions of varying A and f, with blue, green, and orange indicating the three stable configurations. (b) Swimming speed of the pair, compared to the speed of an isolated wing (in black). (c) Speed enhancement of a pair relative to an isolated wing, U/U_0.

can be adjusted, and the resulting steady-state swimming speed U and interswimmer separation distance g are measured by an optical encoder and high-speed video camera, respectively. Typical inputs of $A \sim 0.5$–3.0 cm and $f \sim 2$–4 Hz lead to speeds of $U \sim 5$–100 cm/s for wings of chord length $c = 3.8$ cm. The Reynolds number is high, indicating the dominance of fluid inertia over viscosity: $\mathrm{Re} = Uc/\nu \sim 10^3$–$10^4$, where ν is the kinematic viscosity of water. Use of a clear-walled tank allows for visualization of the flows, and application of external forces to the bodies as they swim allows for the measurement of interaction forces.

Emergent dynamics and configurations. Interactions between the swimmers could have various possible outcomes, such as collision through attraction or separation due to repulsion. When the wings are placed within a few body lengths of one another and flapped, we observe a nuanced interaction in which the separation distance initially changes before eventually reaching a steady-state value which thereafter remains constant. If slightly perturbed from this arrangement, the pair robustly returns, suggesting that the observed configuration represents a stable equilibrium state. If perturbed sufficiently strongly, the pair can be made to arrive at a second state of greater separation, and yet another state can also be found (see Movie S2). We quantify these observations by measuring the steady-state interswimmer distance g across variations in amplitude A and frequency f, as reported in Fig. 2(a). For a given A and f, we have identified up to three arrangements which are colored blue, green, and orange according to increasing g. For fixed frequency, say $f = 4$ Hz (square symbols), the value of g in each state increases with A. Increasing f also leads to greater values of g. Data across all kinematics show that stable states of collective locomotion involve configurations of *discrete* separations. Similar dynamics has recently been found in simulations of self-propelled flexible filaments [24], suggesting that this discretization may be a generic feature of interacting flapping locomotors at high Reynolds numbers.

Figure 2(b) shows the swimming speed U across variations in flapping kinematics, and we include for comparison the speed U_0 of a single wing (black curves). For a single wing as well as a pair in each stable state, the speed increases with both A and f. However, the pair tends to swim faster than a single wing, as shown by the plot of the speed ratio U/U_0 versus dimensionless distance g/c in Fig. 2(c). The speed enhancement can be as high as 25%, which occurs in the first state when the wings are closest. These data indicate that not only does the leader affect the follower, but the follower also drives the leader to swim faster than it would in isolation, and this upstream influence can extend over several chord lengths.

It is natural to view the emergent stable states as predominantly organized by the flow left in the wake of the leader. The leader traces out a wavelike trajectory through the fluid, and the wavelength $\lambda = U/f$ is set by the input vertical heaving and output horizontal swimming. Inspired by recent work on wing arrays of fixed spacing [23], we define a schooling number $S = g/\lambda$ that measures the separation between bodies in units of λ. In Fig. 3(a), we recast the data of Fig. 2

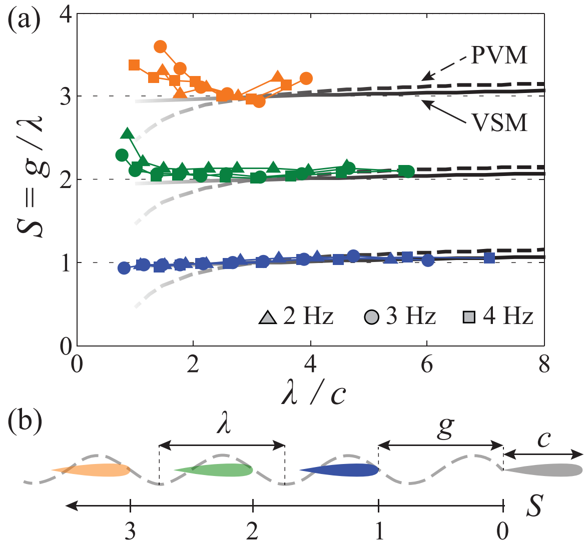

FIG. 3. Interacting swimmers select quantized separation distances. (a) Across all kinematics, the separation g is approximately an integer multiple of the wavelength of motion λ. Predictions from a point vortex model (PVM, dashed curves) and a vortex sheet model (VSM, solid curves) show a similar quantization (see text for details). (b) Stable configurations correspond to integer values of the schooling number $S = g/\lambda$.

in terms of S, revealing a remarkable collapse onto integer values. Stable schooling configurations thus involve interindividual separations that are not only discrete but also *quantized*, with λ serving as the fundamental length scale. This finding is shown schematically in Fig. 3(b), where the observed arrangements correspond to an integer number of wavelengths separating the swimmers.

There are alternative characterizations of the relative positioning, such as the center-to-center distance rather than the gap distance. As detailed in the Supplemental Material [27], the separation distance g seems to provide the best collapse of the data and thus a unified description of emergent stable states. This suggests that the interaction is dominated by the effect of the flow structures produced at the leader's trailing edge on the follower's leading edge.

Flow visualization. The success of the schooling number characterization suggests that the follower interacts coherently with the flow generated by the leader. To reveal these flows, we seed the water with microparticles, illuminate with a laser sheet, and record the particle motions using a high-speed camera (see Movies S3 and S4). In Fig. 4(a), we show a frame captured during the downstroke for the case of a single wing, and these flow path lines reveal an array of vortices left

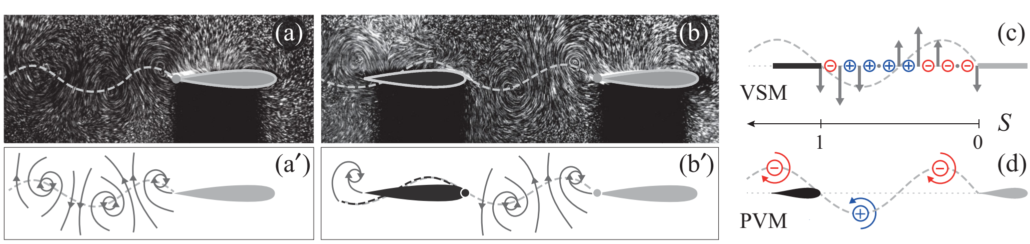

FIG. 4. Experiments and models of wing-wake interactions. (a) Experimental path-line visualization of a single wing swimming and (a′) schematic showing the array of counter-rotating vortices left in its wake. (b), (b′) A wing pair in the first state, in which the leading edge of the follower intercepts vortex cores. Modeling the two-swimmer interaction using (c) a vortex sheet model (VSM) and (d) a point vortex model (PVM).

in the wing's wake. The schematic of Fig. 4(a′) shows how vortices of alternating rotation are laid out along the trajectory, forming the so-called reverse von Kármán wake. This wake is a generic feature of flapping locomotion that has been observed for forward flight of birds and fish swimming [30–33] and has come to be regarded as a signature of thrust generation [25,26,34]. Figures 4(b) and 4(b′) show the corresponding flow fields for the case of a wing pair in the first stable state. A similar chain of vortices is left by the leader, and here the fixed interwing spacing is associated with the repeated interception of vortex cores by the follower wing's leading edge. These observations confirm that coherent wing-wake interactions underlie the schooling states and suggest routes toward understanding the hydrodynamic basis of their stability.

Mathematical models of vortex-body interactions. Guided by these flow observations, we seek models that account for the quantized configurations of interacting swimmers. We consider two models, each of which determines the vortical flow left by the leader and computes the total horizontal force on the follower. As shown in Figs. 4(c) and 4(d), a vortex sheet model (VSM) assumes a continuous distribution of vorticity shed by the leader while a point vortex model (PVM) views this wake as an array of discrete vortices. In both, the flow is 2D and inviscid, with viscosity incorporated solely through the Kutta condition of smooth flow over the trailing edge [35]. Both models compute thrust on the follower but lack a mechanism for drag, and thus the equilibrium swimming speed U—which arises as a balance of thrust and drag—must be prescribed. We impose the speed of the pair to be that of an isolated swimmer, $U = U_0$, and we also assume that the drag on the follower is that felt by an isolated swimmer. Together, these imply that the follower's thrust is that of an isolated swimmer, $T = T_0$, which provides the condition for determining the equilibrium spacings of the pair.

Complete model calculations are provided as Supplemental Material [27], and here we highlight key steps and results. Our VSM is an adaptation of Wu's linear (small-amplitude) theory for the flow and thrust for a flapping swimming plate [36]. The leader is unaffected by the follower and produces the flow of an isolated wing: For small amplitude $A/c \ll 1$ and fast swimming $fA/U \ll 1$, this takes the form of a flat vortex sheet whose strength varies sinusoidally with downstream distance. The vertical flow speed can be shown to oscillate with distance, and we use a similar theory of Wu to compute the thrust on the follower in this wavy stream [37]. The thrust varies sinusoidally with downstream distance, and the condition $T = T_0$ yields a family of spacings whose stability properties are inferred from the spatial dependence $T(S)$. Stable equilibrium solutions are displayed in Fig. 3(a) as the solid curves, revealing values of S near the integers.

Despite its different assumptions, the PVM shows similar results, displayed by the dashed curves in Fig. 3(a). This nonlinear model applies to higher amplitude motions $A/c \sim 1$ and computes the follower's thrust as that felt by a Joukowski airfoil [38] located at the midplane of an array of vortices [39,40]. Here, $T = T_0$ again determines the equilibrium spacings, whose stability can then be assessed. The periodicity of the flow leads to a family of stable spacings, and Fig. 3(a) shows that the model agrees well with experiments in the limit of large A/c and thus large λ/c. Taken together, the agreement of experiments and models suggests that orderly configuration of swimmers does not depend sensitively on details of the flows or body shape but is a generic feature of flapping locomotion in a periodic flow.

These models also offer a qualitative explanation for the stable positioning of the follower, which swims in the alternating up and down flows left by the leader [vertical velocity shown as gray arrows in Fig. 4(c)]. Considering, for example, the middle of the downstroke, as shown in Fig. 4, the follower is near a node or zero-velocity point in this wave. If the follower were slightly displaced closer to the leader, it would flap downward in a downward flow, and the reduced relative velocity would lead to decreased thrust and repulsion away from the leader. Similarly, if the follower were displaced further from the leader, it would flap downward in an upward flow, increasing thrust and thus attracting it to the leader. In both cases, it seems perturbations are resisted and the observed position is a stable one. Similar reasoning suggests that positions near adjacent nodes are unstable, and so not observed in the experiment. Stable states are thus separated by the wake wavelength.

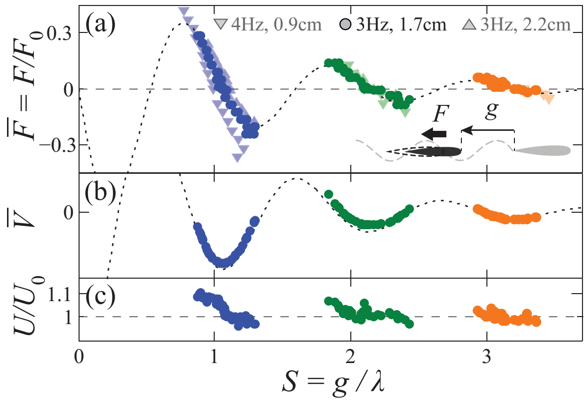

FIG. 5. Restoring fluid force on the follower. (a) Net fluid force F on the follower versus location downstream of the leader g, both axes made dimensionless. The dark data correspond to $A = 1.7$ cm, $f = 3$ Hz, and thus $\lambda/c = 3.2$, and two additional data sets have $\lambda/c = 1.6$ and 4.8. Each data set is normalized by $F_0 = 1/2\rho\mathcal{A}(\pi Af)^2$, the typical force due to dynamic pressure on the wing of planform area $\mathcal{A} = 29$ cm^2. (b) The potential $\overline{V} = -\int \overline{F} dS$ reveals multiple stable wells. (c) Swimming speed compared to that of an isolated swimmer U/U_0. The dotted curves of panels (a) and (b) are guides to the eye.

Mathematical derivations behind these arguments are detailed in the Supplemental Material [27], and both models provide an expression for the wake-induced perturbation to the follower's thrust. It is found that the equilibrium positions are in close proximity to the zero-velocity nodes of the wake, and these equilibria alternate in their stability.

Interaction forces and potential. Our experiments and models reveal multiple stable positions for the follower, and the degree of stability depends on the strength of the hydrodynamic force that tends to restore the follower's position if perturbed. We map out this stability by applying an external load to the follower, forcing it to come to a new spacing g and steady speed U for which the applied force balances the net hydrodynamic force F. We implement this scheme using a mass-string-pulley apparatus that allows for external forces of varying strength and direction, i.e., driving the follower toward or away from the leader (see Supplemental Material [27]). The data in Fig. 5(a) represent the force-distance profile for three sets of kinematics, with both axes made dimensionless (see caption). Considering the first state (blue), no external force leads to $F = 0$ and $S \approx 1$. If driven closer to the leader, then $F > 0$ and S decreases, as shown in the inset. Likewise, if driven further away from the leader, S increases and $F < 0$, again tending to restore the $S = 1$ state. Near each stable state S^*, the fluid force thus acts like a Hookean spring, $F \approx -k(S - S^*)$, and widely separated states have a smaller spring constant k and are thus more weakly stabilized.

The data of Fig. 5(a) also show that the interaction forces can be quite large, as high as one-third of the typical hydrodynamic loading on the flapping body, denoted as F_0 and defined in the caption of Fig. 5. As detailed in the Supplemental Material [27], the models also show stable or downward-sloping force profiles near integer values of S, but the models overpredict the force magnitudes and do not account for its decay with distance.

The force measurements motivate a description in terms of a stability potential. In analogy to classical mechanical systems, we define the potential as the integral of force with distance, which in dimensionless form is $\overline{V} = -\int \overline{F} dS$. Integrating the data of Fig. 5(a) yields the potential shown in Fig. 5(b), revealing a corrugated energy landscape and a sequence of stable wells whose depth diminishes with separation. This potential function also indicates that the gaps in the force profile of Fig. 5(a) are due to instability of these arrangements, and it suggests that $S > 3$ states are not observed because of their exceedingly weak stability. Finally, we note that the speed data of Fig. 5(c) show only small variations under these force perturbations.

Discussion. These findings offer experimental support for the Lighthill conjecture that formation locomotion, or the orderly arrangement of flapping swimmers or flyers, can emerge spontaneously from high-Reynolds-number flow interactions. The multiple stable configurations of tandem swimmers observed here reflect the influence of the leader's periodic flow on the follower, which imposes a quantization of interindividual separation distance into integer multiples of the swimming wavelength. Our mathematical models recover similar equilibria and shed light on the mechanism for the stable positioning of the follower as it flaps within the wavelike flow of the leader. Our models, however, do not account for the decaying stability of states with separation, which is likely due to the turbulent breakdown of vortices and thus may be affected by wing shape and 3D flow effects in our rotational setup. We have also shown that the stabilizing fluid forces are significant over a range of several body lengths, and our interaction potential formulation may prove useful in predicting the dynamics of a collection of swimmers and the response to a perturbation. Indeed, a potential formulation may be the most tractable description of larger ensembles.

Intriguingly, we also observe a speed increase for pairs relative to a single body, indicating an influence on the leader by the follower. Because our models assume a speed and thus cannot shed light on this effect, both validation and more complete explanation likely await more elaborate models or computational flow simulations. Perhaps two nearby wings can be (crudely) viewed as a longer body, in which case the enhancement is consistent with observations that the speed of a single wing increases with chord length [41]. While counterintuitive, we note that upstream effects have been observed for interacting flapping bodies, both active [19] and passive [16].

The locomotion states observed here arise from long-lasting inertial flows, a feature shared with high-Reynolds-number animal collectives, from insect and krill swarms (Re $\sim 10^2$–10^4) to bird flocks and fish schools (Re $\sim 10^3$–10^6). The high densities in these groups suggest that flow effects are considerable [4–7,42]. Direct extrapolation of our results implies that such ensembles would assume latticelike or crystalline arrangements, though it remains for future studies to investigate many-body arrays of free locomotors in 1D, 2D, and 3D configurations. Recent work on wings held at fixed spacing indicates the dominance of nearest-neighbor interactions [23], suggesting that two-body results may extend to the many-body problem. In this case, the springlike fluid forces may lead to collective vibrational modes, akin to phonons in conventional crystals.

The picture of a school as a moving crystal of fish was further developed by Lighthill, who also viewed swarming to schooling as a disorder-to-order phase transition driven by hydrodynamic interactions [15]. Though physically appealing, biological support remains sparse, perhaps due to the difficulty of measurements. To our knowledge, long-range order has not been reported in studies of schools, though it has been shown that, when presented with unsteady flows, fish adopt new swimming motions and synchronize with oncoming vortices [43]. These motions are in fact strikingly similar to those of euthanized fish in such flows [44], suggesting that passive effects play a significant role in the coherent interactions of swimming fish with periodic flows. Recently, measurements of birds flying in V formations and tandem configurations have shown coherence between nearest-neighbor flapping motions [42], which was interpreted as a willful behavioral response that exploits flows. From the perspective of Lighthill's conjecture and the supporting evidence shown here, it may be that such orderly and advantageous collective locomotion is a stable equilibrium state resulting from flow interactions.

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