

Where Physics Meets Behavior in Animal Groups

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This review explores the critical role of the physics of the body and the environment in shaping behaviors within the emerging field of the physics of social interactions. We revisit the intriguing case study where a dead fish, lacking neural control, appeared to swim upstream, propelled by its body resonating with vortices. This example expanded the conventional view of behavior as solely a product of biological processes, underscoring the significant influence of physical forces on living and nonliving entities alike. We build upon this foundational understanding and review how the physical characteristics of individual organisms interact with other individuals and with their environments to produce complex group dynamics, focusing on key examples: hydrodynamic interactions in fish schools where individual movements are influenced by water flow and collective swimming patterns; thermoregulation in penguin huddles, where individuals closely pack to minimize heat loss and optimize energy use in harsh climates; and raft formation in ants as a survival strategy during floods, leveraging their collective buoyancy and waterproofing properties. Our discussion emphasizes the importance of considering both the physics of the bodies and the environmental factors in understanding these intricate dynamics. By combining findings from a range of taxa to showcase the interplay between physical and biological aspects of collective social behaviors, we hope to encourage further research that explores their many facets and implications.

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I. INTRODUCTION

The study of animal behavior, rich in its complexity and scope, encompasses an understanding of how the physical bodies of sentient beings interact with the physical world and, importantly, with one another through social interactions [1–3]. These social interactions are fundamental to the survival and reproductive success of many species, facilitating essential behaviors such as defense against predators, resource sharing, and mating. Social interactions, even at short-length scales, can drive collective behavior observable on much larger scales, as evidenced in phenomena like bird flocking [4,5] and insect swarming [6–8]. These natural spectacles, which have fascinated humanity for centuries, showcase the complex dynamics of group behavior emerging from simple, localized interactions [9–11].

In this review, we explore physics models that provide insights into social interactions, particularly those driven by the physical attributes of an organism and its environment, rather than behavior that arises from conscious choice, i.e., solely as a consequence of neuronal activity. This also stands in contrast to models that abstract behavior such that it can be considered to occur “in a vacuum,” such as the Vicsek model [12]. We demonstrate how traditional theories designed

for inanimate systems can fall short when applied to living systems, but that these shortcomings can, in turn, be used to identify missing behavioral components critical to an understanding of such living systems [13]. Such an approach offers a pathway to reverse-engineer these absent elements, thereby deepening our understanding of the system’s dynamics. From this exploration, a new subfield emerges: the physics of social interactions. This area sheds light on the fundamental physical principles that govern group behavior, unveiling profound insights into the complexity of the natural world.

Applying a physics approach to control and isolate various aspects of a system presents notable challenges, especially with living animals. Rarely can we distinctly separate active from passive behavioral elements. However, the unusual case of the swimming dead fish, as studied by Liao [14] and Beal *et al.* [15], offers a compelling example. This study highlights an unexpected overlap between inanimate and animate matter, revealing that a dead fish can appear to swim: The fish’s pliable body synchronizes with a vortex wake in a flow of water, propelling it upstream. This discovery contributed to the evolving understanding that behavior is not exclusively driven by conscious choice (e.g., a decision to activate certain muscles, based on neural processing) but also critically influenced by physics. Indeed, more recent work has revealed universal principles governing the locomotion of inertial aquatic swimmers across various sizes and taxa, including scaling laws linking swimming speed to tail beat amplitude and frequency [16,17]. These results at the level of individual animals highlight the importance of viewing the bodies of animals and the spaces between them not as discrete entities but as continuous

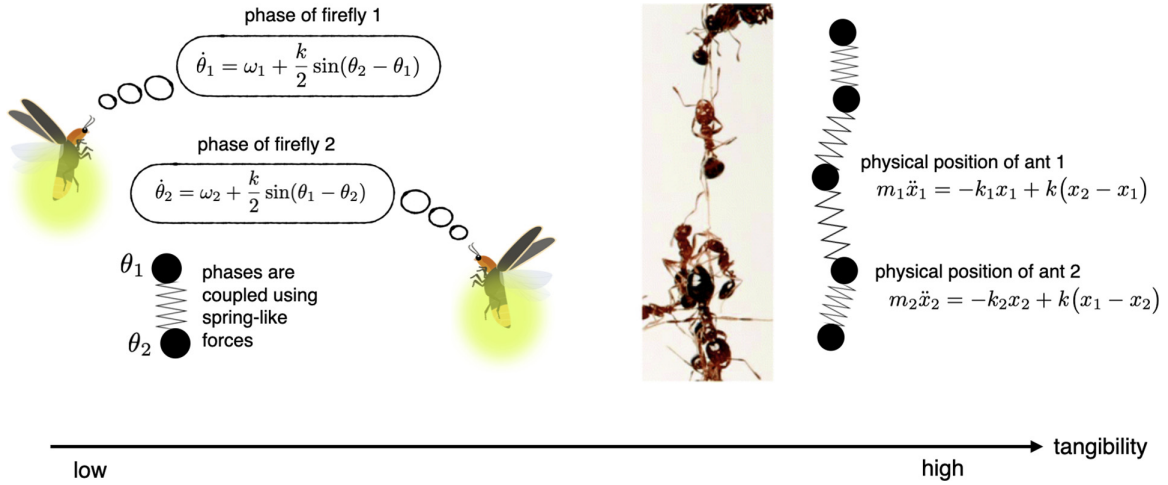


FIG. 1. Models of social interactions in living systems can be examined on a scale of tangibility. On the low end (left) are those that link the biological system with a physical system strictly by way of analogy: For example, the synchronized flashes of fireflies, which are controlled by neuronal activity, are described as coupled oscillators, as shown by the equations of the Kuramoto model [20] (θ_i and ω_i are the phase and frequency of firefly i , respectively, and k is a coupling constant). At the high end (right) are systems that can be modeled more explicitly using physical constructs, even if simplified. Ants link their legs together into bridges and bivouacs, forming an elastic material. The body-body connections are straightforwardly represented by connected springs, and the equations of motions of ants can be written using Hooke's law. Ant image in Ref. [21] (x_i , m_i , and k_i are the position, mass, and spring constant of ant i respectively, and k is a coupling constant).

materials that interact dynamically with one another. While there is also a rich body of work on how physical interactions underlie the collective dynamics of microorganisms like bacteria [18,19], in this review, we focus on animals with brains, as the intersection of behavior, physics, and social dynamics in this regime presents a complex and fascinating challenge that is only starting to be unraveled.

Such reports about the dynamic interaction between an organism's body and its environment lead us to a broader examination of models of animal behavior that integrate physical principles, make testable predictions, and bring a deeper understanding of social interactions. Many of these models exist on a scale of what we refer to as tangibility (Fig. 1). At one end of the scale are models that build an analogy between social and physical forces, such as the fluid mechanics models of traffic flow [22], the spin model of bird flocking [23], or the coupled springs model of firefly synchronization [24].

To clarify the tangibility distinction, let us consider the latter example. Fireflies are not literally connected by physical springs, yet in the model, their social behavior via flashing is reflected by the principles of coupled elastic springs dynamics. In contrast, and on the other end of the spectrum, is the example of ants physically linking themselves via their elastic limbs into large swarms [25]. They effectively form a “material made of ants,” thus creating a tangible elastic material. While many systems fall at various points on this spectrum, in this review, we focus on models at the more tangible end of the spectrum, driven by reimagining bodies and spaces as dynamic continua.

In the following sections, we build on the initial dead fish study and discuss how fish behavior, from energy-saving maneuvers to cohesive schooling [Figs. 3(a)–3(c)], demonstrates the intertwined nature of biology and physics. By examining these phenomena, we gain insights not only into the behavior of fish but also into the broader question of how

animal behavior weaves together sensory input and biological motivation with the physics of the organisms' bodies and their surrounding environment (Fig. 2). Next, we explore two examples of dense aggregations analogous to inanimate physical systems. By examining how the biological systems differ from the inanimate systems, we disentangle the effects of physical forces from social behavior. The first example concerns emperor penguin colonies in Antarctica forming dense huddles for warmth [Figs. 3(d)–3(f)]. Their phase transition dynamics resemble that of colloidal gelation [26], but physiological requirements motivate penguins to continuously shift in a coordinated manner to redistribute heat. The second example pertains to fire ants that create dynamic rafts and towers during floods; collective structures repel water more effectively than individual ants [Figs. 3(g)–3(i)]. Together, these examples indicate how physics and social behavior manifest interdependently.

II. HOW HYDRODYNAMICS KEEPS FISH GROUPS SWIMMING

Many species of fish swim collectively in massive schools, which offer protection from predators and enhanced foraging and mating success [Fig. 3(c)]. Here we explore the interplay between conscious choice and body-environmental physics (Fig. 2) that arise in fish schools. Recent studies have indicated that hydrodynamic interactions can shape a large part of what we observe in groups of fish, just as these interactions can allow a dead fish to “swim” [27–29] [Fig. 3(b)]. Moreover, the collective behavior of a fish school can potentially exert changes upon the surrounding fluid to provide energetic benefits to the individuals within [30]. Simulations, robotic studies, and experiments with pairs of fish have indicated that moving together allows fish to swim more efficiently [31–34], and the specific hydrodynamic effects that impart these advantages

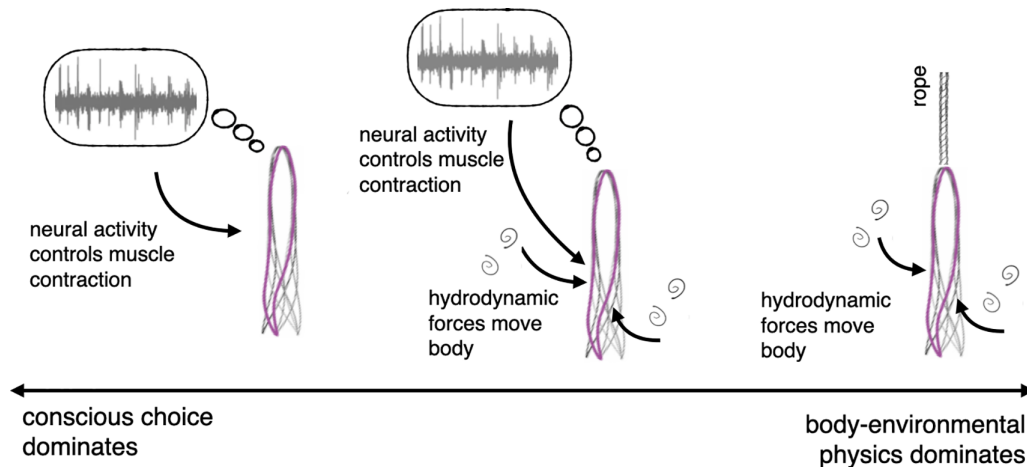


FIG. 2. The behavior of an animal is can be dominated by conscious choice or by the body-environmental physics, or it can be governed by a combination of the two. In environments devoid of naturalistic fluctuations (such as turbulence), conscious choice can play a primary role (image of neural activity from Ref. [61]). In the limit of the lack of conscious choice, body-environmental physics dominates: The cartoon illustrates how a dead fish appears to move as if pulled by a rope, when hydrodynamic forces propel the body. In between the limits, a feedback loop arises between conscious action that imparts changes to the environment and the environment in turn affecting the body.

have been identified for fish swimming in line and side by side [32,34].

Several studies have directly quantified the energy expenditure of fish swimming in schools by using respirometry to measure oxygen consumption [35–37]. Kinematic measurements of tailbeat amplitude and frequency are often used as proxy for measuring energy consumption, but kinematics does not necessarily correlate with energy consumption [30]. In one recent study, Zhang and Lauder compared the oxygen consumption of fish swimming in schools with that of individual swimmers, confirming that swimming in schools saves energy [35]. The authors observed that fish schools experienced up to a 56% reduction in energy expenditure per tail beat compared to fish swimming individually, and fish in schools also recovered more quickly after high-speed swimming than individual fish.

It was also observed that while fish maintained a relatively consistent separation between one another, individual fish regularly changed their positioning throughout the group. Early studies of the hydrodynamics of fish schooling postulated that fish swam in a diamond formation to minimize energy cost [38], but the energetic benefits of schooling were subsequently contested [39], as fish do not maintain the consistent positioning and spacing required to extract the advantages of the diamond formation. However, our contemporary understanding of schooling hydrodynamics has elucidated the range of energy-saving effects that can occur depending on the relative positioning between fish and the absolute position of fish within the group [40,41]. Respirometry measurements by Killen *et al.* showed that fish with lower aerobic capacity swam at the back of schools, moreover exerting fewer tail beats to keep up with the leaders [36]. Those with higher aerobic capacity were able to withstand the drag at the front of the schools and in return had greater access to food. Similarly, Herskin and Steffensen also found that fish at the rear of a school had a 9–23% reduction in oxygen consumption and a 9–14% lower tailbeat frequency [37].

The intentionality in fish behavior (illustrated on the left side of Fig. 2) becomes apparent when fish exploit these energy-saving effects by actively positioning themselves and altering their swimming kinematics to lower energy costs. Fish can position themselves when in the presence of an oncoming wake in order to save energy: For example, fish will swim between vortices of a drag wake, which decreases muscle activity [42]. Moreover, a fish swimming behind another fish will swim directly into the wake produced by that fish [43]. They also synchronize their tailbeats to match the leading fish to further swim more efficiently; this behavior has been shown to lead to a reduction in energy costs [29]. Interestingly, it was found that even visually or lateral line (the mechanosensory organ system that senses fluid flow and pressure gradients) impaired fish could perform this action. A subsequent study proposes via simulation that fish could optimize their tailbeat rate solely through proprioception [44].

Intriguingly, several studies have suggested that fish can remain paired or grouped with others without the need for sensorimotor control. This has been probed with robotic structures that swim like fish and with fish that have had their visual or lateral line systems reversibly impaired [45–49]. For example, it was observed that two inanimate foils can move together cohesively due to the flow creating stable configurations in which the foils neither collide nor separate, even if they have different, uncoordinated swimming kinematics [46], and can swim side by side if their kinematics are out of phase but synchronized [47].

Hence, as an extension to the dead fish example, it is often assumed that (live) fish in a school process visual cues to actively maintain their position relative to other fish. While sensing indeed promotes enhanced group function, it is possible for what we observe as collective behavior to arise in part from passive physical forces. Indeed, the conjecture that cohesive fish schools can form purely through passive hydrodynamic forces originates from the 1970s, when James Lighthill postulated that coordinated arrangements could arise

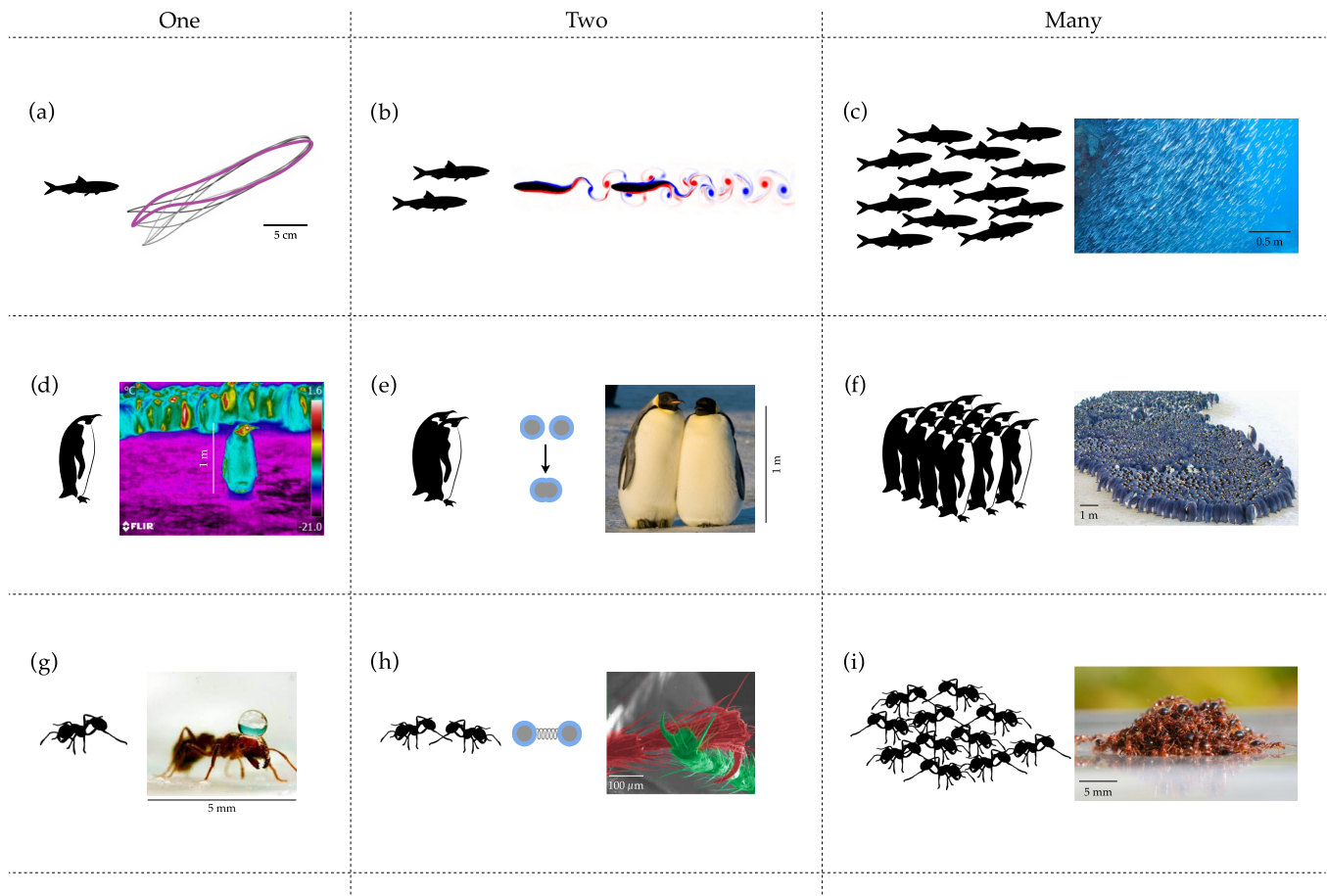


FIG. 3. Physics is woven into the fabric of animal behavior over scales ranging from a single individual to a pair of individuals to a collective. (a) Fish have flexible bodies that can undulate as they swim, and even a dead fish can extract energy from vortices to produce thrust. Fish outlines adapted from Ref. [53] (outlines represent different body configurations over the course of one undulation period; one configuration is highlighted in violet for clarity). (b) A pair of fish create and interact with each others' vortices and can remain paired via passive hydrodynamic interactions. Red corresponds to positive vorticity; blue, negative vorticity. Image from Ref. [54]. (c) Many species of fish swim together in massive schools for enhanced survival benefits; swimming together has also been shown to reduce energy costs compared to swimming alone. Image by Matthew Hoelscher, Wikimedia Commons. (d) Thick plumage helps protect an emperor penguin from the cold, but it still loses heat readily through exposed surfaces and must maintain a high metabolic rate to stay warm. The color scale corresponds to body temperature. Image credit Ancel/IPEV/CNRS (used with permission). (e) Penguins pack closely together to decrease the exposed surface area, as shown in the diagram. Image by Samuel Blanc, Wikimedia Commons. (f) Penguin colonies form massive huddles, resulting in higher than a 50% reduction in metabolic rate. Image from Ref. [62]. (g) A single fire ant's cuticle is moderately hydrophobic. Image from [25]. (h) Ants latch onto one another to form self-assemblages such as the rafts that float on top of flooded areas. A pair of ants (one is highlighted in red and the other in green) join tarsi, creating a springlike connection, as illustrated by the diagram. Image from Ref. [25]. (i) Collectively, the raft experiences increased hydrophobicity and traps air pockets that allow the ants to breathe. Image from Ref. [25].

as a result of passive flow-mediated interactions without active control, in the way that crystals form via intermolecular forces [50]. Thus, a nuanced exploration of physics demands explicit consideration of the environment as an integral element shaping agents' interactions, in addition to strategic or otherwise cognitively driven behavior. While previous studies and models often focus on vision-based and distance-based interactions [51,52], the role of the fluid environment was frequently overlooked due to computational challenges, but recent work has explicitly modeled hydrodynamic interactions with fish [53,54]. Moreover, robotic experiments can experimentally decouple behavior from physics [45,47,55]. Advances in robotics and modeling has enabled the Lighthill conjecture to be revisited and further developed: Ramana-

narivo *et al.* find in experiments that a pair of self-propelled wings spontaneously form arrangements that are robust to perturbations and move faster than a single wing [56], Dai *et al.* perform simulations of undulating swimmers and identify emergently stable configurations [57], and Peng *et al.* simulate groups of flexible flappers and observe that hydrodynamic forces act as restoring forces to promote group cohesion [58].

Finally, we highlight a recent study by Zhang *et al.* that put forward a remarkable hypothesis as to how the interplay between a fish school and the surrounding fluid imparts energetic benefits [30]. This study tested the energy expenditure of danio fish schools swimming at not just a range of speeds but different fluid environments: turbulent and laminar flows. Fish in schools expend less energy in turbulent conditions

than swimming alone (about a 70% energy reduction), but no difference was observed between the school and the individual in laminar conditions. Schools in turbulence also reduced their volume by over 40%. Fish beat their tails more rapidly and strongly, and consumed more oxygen, when swimming individually in turbulent flows compared to laminar flows, but they did not change their tailbeat when swimming in schools. We note, though, that this result stands in contrast to the observations of van der Hoop *et al.*, who examined individual shiner perch in varying flow conditions [59]. Shiner perch were observed to consume more oxygen in low-turbulence flows than high-turbulence flows. Moreover, at very high tailbeat frequencies, oxygen consumption increased more sharply as a function of tailbeat frequency for low turbulence than high turbulence, while this is observed to be the case for high rather than low turbulence in Zhang *et al.* [30]. van der Hoop *et al.* posit that fish in turbulent conditions, which demonstrate greater positional variability, may in some way leverage the high variability of turbulent energy through space and time. However, the mechanism by which this is attained is yet to be characterized, and future studies are needed to fully contextualize fish behavior across group sizes and species in a wide range of naturalistic conditions.

Zhang *et al.* also observed that individually swimming fish oscillated their heads regularly in laminar flows, but this movement became irregular in turbulent conditions. However, in schools, fish demonstrated regular head oscillations even in turbulent flows. This lead to the hypothesis that fish schools act to shelter the interior fish from turbulent conditions outside, and that the behavior of the school creates calmer flow conditions inside. The extent to which the head movements of fish, along with the tailbeat as described in the previous paragraph, are driven by passive physical forces is not clear; cognitive control may also drive these behaviors as a response to the hydrodynamic environment. Moreover, the head movements may not merely be an inadvertent consequence of undulation but might enhance sensing and optimize respiration [60]. The ongoing mystery of how sensing, cognition, physiology, social interactions, and hydrodynamics of the fluid environment converge within a fish school is a prime example of the exciting open questions that arise from the convergence of biological function and physical forces.

III. EMPEROR PENGUINS RESIST JAMMING DURING COLLECTIVE THERMOREGULATION

We draw a parallel between fish schools and penguin huddles, another system whose social interactions are influenced by the physics of the interaction between animals and environment. While in the previous section the social interactions were guided by hydrodynamics, penguins' social bonds are governed by the principles of thermodynamics, specifically through the management of heat loss to the surrounding air. Emperor penguins live in colonies of several thousand individuals in harsh Antarctic environments where temperatures can regularly fall below -40°C in the winter [63,64]. To stay warm, penguins pack together into massive dense aggregations, consisting of up to several hundreds or even thousands of individuals, known as huddles [Fig. 3(f)]. Huddling

reduces heat loss and overall energy expenditure by decreasing the exposed surface area and raising the local ambient temperature [Fig. 3(e)] [65–70]. Penguins lose heat from their body via several means, including radiation, convection (especially in windy environments), and conduction (via body parts that are in contact with the ground) [71,72]. Heat loss is usually modeled as a linear function of exposed surface area, which underscores the efficacy of huddling in minimizing this loss. About half of the total heat loss occurs through the penguin's trunk [Fig. 3(d)], which comprises over 80% of the penguin's total surface area [72]. By huddling, penguins can reduce their exposed surface area by up to 74% [65]. Huddles also raise the local ambient temperature by at least 6°C , and members can achieve an approximately 50% reduction in metabolic rate [65].

A penguin colony can be described as having two possible states: a nonhuddling, fluidlike state, and a dense, solidlike, huddle state. The phase transition was described by Richter *et al.* [73] to occur at a critical value of “apparent temperature,” which is a linear combination of ambient temperature, wind speed, solar radiation, and relative humidity. Zitterbart *et al.* further drew comparisons between penguin aggregations and colloidal particles interacting via short-range attraction potentials [26]. Colloids form gels by kinetic arrest: When the volume fraction and/or the strength of the attraction is increased, the colloidal particles become increasingly crowded and form a gel. Likewise, harsh environmental conditions increase penguins' effective short-range attraction, bringing them closer together, and spurring the transition to a solid-like huddle state. Crucially, in a deviation from the gelation analogy, it was also observed that penguins regularly take small coordinated steps, approximately every minute, with this behavior spreading throughout the huddle in a traveling wave [26]. This prevents jamming in the huddle, facilitates a flow of penguins at the colder exterior into the warmer interior, and allows smaller huddles to combine into larger ones. Such behavior separates the penguin huddle from the inanimate colloidal model, demonstrating how examining a living system through the lens of physics reveals intentional social behavior that promotes biological survival.

Ultimately, a full understanding of the dynamics of penguin huddles requires analyses that combine both movement and heat transport. Two recent modeling studies examine the macroscopic evolution of the huddle by explicitly accounting for individual penguin reorganization. First, Gu *et al.* [67], developed a coupled fluid-behavior model that integrates the full Navier-Stokes equations for wind field analysis with a smoothed particle hydrodynamics approach to simulate individual penguin behavior within huddles. By treating penguins as individual particles, the study reveals how behaviors aimed at maximizing individual fitness dynamically interact with environmental forces. The model predicts that a low-density collection of up to 800 “penguin” particles will pack into a dense, stable oval shape and furthermore recapitulates the traveling waves that redistribute individuals throughout the huddle. Since the “penguin” particles only seek to improve their individual outcomes, the model stipulates that the perceived communal huddling behaviors emerge from individualistic actions influenced by the surrounding physical environment.

Another recent study, by Harris and McDonald [74], represents penguins as a continuum for the first time rather than modeling each penguin as an individual particle. In this approach, it is assumed that heat transfer from the exterior follows an advection-diffusion equation, while the penguins are packed densely enough that wind does not flow through the interior, and penguins instead generate body heat that diffuses through the huddle. The authors found that any initial starting configuration would evolve into a steady-state egg-shaped huddle; the higher the Péclet number (Pe), the more elongated the shape (with the huddle becoming circular in the limit of no wind, or $Pe = 0$). Meanwhile, the larger the effect of penguins' interior redistribution, the more circular the huddle would become. Together, these recent modeling efforts represent important advances in quantifying the macroscopic dynamics of a collective in complex, harsh environments. Further experiments to confirm the predictions of these models remain to be performed and may as yet reveal new discoveries about this unique living system.

IV. FIRE ANTS FORM ELASTIC, HYDROPHOBIC AGGREGATIONS IN TWO AND THREE DIMENSIONS

Physical interaction with the environment is also critical in fire ants. Their social cohesion and survival strategies are mediated by hydrophobic interactions at the water's surface, showcasing a remarkable adaptation to environments at the interface of water and air.

Fire ants are social insects that live in colonies comprising over 100 000 individuals. They can self-assemble into impressive geometries for survival, such as meter-wide rafts that float on flooded surfaces, and towers that exceed 30 ants in height. Ants grip one another with their mandibles, claws, and sticky pads on their legs, and the ant-ant connection can be readily modeled as a Hookean spring [21], frequently pulled in tension in formations such as bridges and bivouacs.

Recent studies have examined aggregations of fire ants as examples of far-from-equilibrium active matter which reproduce phenomena observed in inanimate systems but with key departures from physical theory motivated by their social activity [75,76]. The aggregation of freely moving ants into clumps of varying densities is akin to motility-induced phase separation (MIPS) [75], which is observed in nonequilibrium systems of self-propelled particles, such as Janus colloids. MIPS occurs when particles accumulate in regions of slower movement, leading to the emergence of coexisting dense and dilute phases [77]. In confined spaces, ants form two phases, with dense "droplets" of slower-moving ants embedded in a lower-density, gaslike phase of faster-moving ants. However, a deviation from MIPS theory is observed in the ant system: Although it was expected that increasing the overall density of ants would alter the proportion of the two phases while keeping the density within each phase unchanged [78], it was found that increasing the total density led to an increase in the density of both phases. This divergence is attributed to the social interactions among ants: As density rises, ants restrict their interactions to maintain a constant number of interactions, representing a notable behaviorally driven departure from inanimate systems that interact with all other particles through physical or chemical potentials.

In a subsequent study, density waves were observed to propagate through a collective of ants confined in a quasi-two-dimensional (2D) column [76]. As the wavefront approached, ants would align themselves with their neighbors. The waves were associated with ants' activity cycles: Ants generally exhibited little activity, with bursts of high activity that precipitated the waves. These activity bursts originated in the densest parts of the ant column, creating an activity cycle that spread throughout the rest of the group. Activity cycles may also be attributed to the intermittent formation of protrusions in fire ant rafts, as discussed below. Moreover, the speed of the waves increased with density, which the authors attributed to a dependence of an ant's speed on the number of its neighbors.

These waves also demonstrate similarities to sound waves in active fluids [79] and traveling polar bands of self-propelled particles [80], but, unlike the latter, local polarization was not dependent on local density. In the densest regions of the ant collective, the ants not active in the wavefront could remain unpolarized as long as they were inactive. These results further establish how living collectives can possess deep similarities with nonequilibrium inanimate systems but point to biologically prescribed activity and social interaction rules as bases for the similarities as well as divergences.

The fire ant raft in particular exemplifies the enhanced functionality that arises from collective interactions [Fig. 3(i)]. An individual fire ant's cuticle is moderately hydrophobic, allowing the ant to trap an air pocket around its body to prevent sinking. This hydrophobicity is quantified by a contact angle of about 102° formed by a water droplet on the ant's exoskeleton [25] [Fig. 3(g)]. When ants link their bodies together into rafts of hundreds or thousands [Fig. 3(h)], the contact angle increases by about 30%, reaching approximately 133° , signifying a higher level of hydrophobicity. This can be explained by the Cassie-Baxter law of wetting, which states that the contact angle increases for rougher surfaces [81]. Forming rafts enlarges the air pockets trapped in and around the ants, significantly reducing the raft's average density compared to that of a single ant. This enables even the ants at the bottom of the raft to breathe. Moreover, when the raft experiences mechanical perturbations, ants contract their muscles (i.e., increase the bond's spring coefficient) to bring their bodies closer together, increasing stability at the cost of decreased buoyancy.

In a later study by Ko *et al.* [82], the formation of fire ant rafts was examined through a unique lens that combines experimental observations with numerical modeling, revealing a sophisticated interplay of physical forces. Despite the ants' propensity for individualistic behavior marked by active repulsion, their collective formations are stabilized by the Cheerios effect—a physical phenomenon where capillary forces attract small floating objects to each other. This study uncovers that rafts disband if they consist of fewer than 10 ants, pinpointing a critical group size for achieving stability. The dynamics of these formations are encapsulated within a Langevin model, highlighting the critical balance between ant repulsion and cohesive capillary forces, offering profound insights into the physics governing natural swarms and their structural stability.

Like penguins, ants, too, move and mix within these rafts. Wagner *et al.* [83] observed that ant rafts spontaneously

formed fingerlike protrusions at the edges, which could potentially allow the group to explore its environment and find dry land. The authors simulate ants as agents in a network, mimicking the monolayer that forms the raft's structure and a separate layer of motile ants moving atop it. By adjusting parameters like detection radius and persistence length based on experimental data, the study reveals that these protrusions, and the overall "treadmilling" behavior of ants moving between the layers of the raft, emerge spontaneously from the interactions of ants within this system. The research highlights the role of increased ant activity in driving the growth of exploratory protrusions, offering additional insights into the collective behavior and structural formation of ant rafts.

Moving from mixing in 2D rafts to mixing in 3D towers, Phonekeo *et al.* [84] delved into the physics underlying the construction of towering structures by fire ants following floods. These structures, which can house thousands of ants, are compared to bell-shaped towers like the Eiffel Tower, designed for equal load distribution. However, unlike nonliving human-made towers, living ant towers are dynamically constructed through a trial-and-error process, constantly adapting until a stable structure emerges. This process is meticulously documented using high-speed and x-ray videography, showcasing a continuous cycle of sinking and rebuilding. By integrating behavioral observations with physical measurements of adhesion, a model predicting the growth rate of these towers as a function of support diameter was developed.

V. DISCUSSION

In this review, we explored social interactions in three disparate living systems, drawing comparisons with inanimate physical systems and illustrating how passive physical forces can play an important role in shaping their collective behavior. The distinctions between these biological and physical systems provide a unique lens through which we can investigate how biology is underpinned by physical considerations. By doing so, we can distill the social motivations that separate living systems from inanimate ones. We do not claim here that hydrodynamics, thermodynamics, and other physical aspects are the sole drivers of interactions in these living systems. Cognitive control mediates behavioral responses to passive physical forces and can enable strategic exploitation of beneficial physical effects. Rather, we advocate for models and studies of collective behavior to incorporate their influence with greater fidelity, as this may enable the untangling of physical effects from conscious action and yield deeper insight into the underlying factors of social phenomena.

Physics intricately intertwines with complex living systems across various scales, influencing individual responses, pairwise interactions, and collective outcomes on a macroscale. The study of collective systems often adopts a "bottom-up" approach, elucidating local interaction rules (e.g., pairwise or nearest-neighbor interactions) to explain emergent global phenomena. Since the early 1980s, models describing flocking and collective movement, largely independent of species, have been formulated [12,51,85,86]. These models typically posit short-range repulsion and long-range attraction among group members, along with alignment of direction, described

as "social forces" acting locally without global control or leadership. Adjusting the scales of these interactions results in diverse flock shapes and dynamics, explaining various observed behaviors.

However, these interaction rules can vary greatly across species and in different environments, and often the physics is neglected. Ling *et al.* examined both pairwise interactions in jackdaw flocks as well as global flock-level behavior to observe that long-range attraction was much stronger perpendicular to the direction of travel than parallel to it [87]. Furthermore, they observed that birds avoided collisions not by speeding away (in the same direction of travel) but by turning away, and by measuring birds' wingbeat frequencies, they determined that turns were less energetically costly than speeding up, at least in air. Together, this resulted in a flock that was elongated perpendicular to the global direction of movement, unlike fish schools, which tend to be elongated along the direction of movement [88]. Unlike in air, in water, it is more energetically advantageous to speed up along the direction of movement to avoid collisions than to turn, which could also explain the difference in group shape [87]. This example underscores the importance of understanding the physics governing individual behavior and its manifestation at the collective level. In other words, it cautions against solely abstracting interactions as "social forces" without considering the physics involved.

The intertwined nature of the physics of the body and the environment with behavioral and social dynamics strikes a parallel with the concept of embodied cognition in neuroscience [89], which views cognition as inseparable from the body and its sensorimotor interaction with the environment. Moreover, the concept of embodied *social* cognition analyzes social interaction through the lens of embodiment: Social stimuli produces both cognitive and bodily affects, and bodily postures and expressions in turn modulate cognitive states and social stimuli [90,91].

The paradigm of stigmergy, originally applied to insects [92], can describe social behavior embedded in a physical environment across species and scales. The concept of "fluid stigmergy" has been proposed by Ko *et al.* [27] as a framework to understand how hydrodynamics mold fish school interactions. Fish, in their swimming, generate a wake that persists in the fluid, akin to the pheromone trails left by ants: In the canonical example of stigmergy, ants implicitly interact with one another by following, reinforcing, and responding to the pheromone trails laid by colony mates. Likewise, a fish's wake contains information about its movements, influencing the behavior of other fish in a collective manner. This framework embodies the perspective of the animals within their environment as a dynamic continuum.

To gain a deeper insight into the living world, we can leverage our understanding of condensed matter (e.g., colloidal gels) and fluid mechanics to disentangle physics and behavior. This approach enables us to comprehend how individuals actively respond and interact with changing environments, extending known physical models to incorporate behavior and fostering a new physics of interacting living systems. The key lies in a systematic and holistic approach, considering individual responses to stimuli, interactions at the pair or small group level, and the collective level, while

recognizing the environmental influence shaping both physics and behavior.

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DATA AVAILABILITY

No data was used or generated in the creation of this paper.

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