

## Dynamics of animal systems

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### 1 Introduction

Consider a fish. It moves effortlessly through water, undulating its body to move forward efficiently, while using its lateral line system to sense and align with the ambient flow [1]. Its agile locomotion is tailored to capitalize on the environment in which it moves [2,3] through a complex behavioral repertoire [4,5]. In a school, multiple fish swim in unison, like a single entity, which could be described through a seemingly simple set of interaction rules [6–9]. If a predator strikes, the information quickly travels through the group [7,10,11], which adaptively morphs itself out of the direction of attack. These fascinating and unique capabilities are reflected in ingenious robots designed to capture desired aspects of the fish [12], for example, the style of locomotion or the information shared through social interactions.

The dynamics of animal systems includes the study of how animals move, navigate their environment, and interact with each other. Systems of biological organisms display an array of complex motion patterns and collective behaviors, and individuals sense each other and their environment through different communication channels [13–17]. These systems operate over a wide range of spatial and temporal scales, thus motivating their study towards solutions to problems across disciplines. Vice-versa, solving related problems in other fields may complementarily inform the study of biological systems.

A diverse set of problems in dynamical systems is motivated by empirical studies on animals. These include biomechanics of locomotion, population dynamics of predator-prey groups, collective motion of animal aggregations, structure and function of neural networks, and biological rhythms of coupled oscillators [18–23].

The ideas underlying this topical issue were inspired by the success of a two-part mini-symposium at the 17th U.S. National Congress on Theoretical & Applied

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Mechanics in East Lansing, Michigan, USA, to which a subset of the authors of this issue contributed. This highly interdisciplinary issue covers theoretical and experimental research that falls under the broad heading of the dynamics of animal systems.

Papers in this topical issue are categorized into three areas of interest: physics of locomotion, where the mechanics underlying the locomotion of organisms is studied; physics of social interaction, which covers mathematical models and analysis of collective animal behavior and predator-prey interactions in nature; and applied physics and robotics, which involves the design of engineering systems that are inspired in their form and function by animals.

We hope that this collection will generate significant interest among the physics, mathematics, biology, and engineering audiences of the journal. Junior researchers might also find this collection useful as an inspiration to initiate graduate study in this emerging and exciting field of research.

In what follows, we first frame the general concepts for each area of interest and then highlight the content of each paper as summarized by the authors. We then draw the readers' attention to some open questions that, based on this collection and our own line of research, should be relevant to the general audience of this journal.

## 2 Physics of locomotion

Through evolutionary processes, each organism—from the unicellular paramecium to the echolocating bat—has acquired unique behaviors and form to navigate [24]. The physics of their locomotion can improve our understanding of their interactions with the environment [25]. Examples include the unique turning mechanisms of species of microorganisms and the diverse ways in which flight has been achieved across insects, birds, and bats via convergent evolution.

The section begins with a review by Brumley et al. [26], who analyze selected physical processes in the ecology of microorganisms. The authors consider the rich physical interactions between microbial motility, flagellar dynamics, and ambient fluid flows. They present several examples where methodological approaches (microfluidics, dynamic imaging) and physical frameworks (mechanics, low Reynolds number fluid dynamics) have shed light on the underlying dynamics, illustrating the depth and breadth of contributions that physics can make to microbial ecology.

Next, Hatton and Choset [27] provide a tutorial showing how ideas from geometric mechanics can be used to capture the physics behind self-propelled locomotion undertaken by animals and micro-organisms. In particular, the authors employ Lie group theory and differential geometry formalism to provide a broader perspective on two common attributes of animal locomotion, that the animal: (1) generates thrust by changing shape to push against its surroundings, and (2) can break the symmetry of its interactions with the environment, enabling it to extract net displacements from cyclic changes in shape.

Huang and Kanso [28] explore the intrinsic self-oscillatory behavior of an insectile wing model, consisting of two rigid wings connected at their base by an elastic torsional spring. The authors start from the hypothesis that the maximum power output of insects' flight muscles is insufficient to maintain observed wing flapping frequencies, without the storage of elastic energy. Three types of behavior are identified in the study: end-over-end rotation, chaotic motion, and periodic flapping. The fact that periodic motion is favored by increasing the stiffness is consistent with the observation that flight muscles and wings are stiff, and suggests that insects can maintain periodic flapping for a range of operating conditions by adjusting their muscle stiffness to the desired energy level.

In the framework of geometric mechanics, Tallapragada and Kelly [29] introduce a model of vortex shedding to achieve propulsion in aquatic environments inspired by animal locomotion. The authors define swimmers whose propulsion is driven by an internal momentum wheel. Vortex shedding depends essentially on fluid viscosity, but its influence can be modeled in an inviscid setting by introducing localized velocity constraints to the swimmers interacting with ideal fluids. Through simulations, the authors demonstrate that a class of these constraints is sufficient to enable self-propulsion with very limited actuation. The swimmer's solitary actuator underscores the symmetry breaking role played by vortex shedding in converting periodic variations in angular momentum to forward locomotion.

Bookending the section with the locomotion in micro-organisms, Zhang et al. [30] investigate the energetic benefit on the Paramecium locomotion from its body asymmetry. The authors combine particle image velocimetry and the boundary element method to develop a model of the fluid motion around a swimming Paramecium. Their results show that the body asymmetry may lead to an increased fluid flux into the Paramecium cilia layer and thus increase the feeding efficiency.

### 3 Physics of social interactions

Many animal species demonstrate some kind of cooperative behavior to perform a task, which would otherwise be impractical or sometimes not feasible for a single individual [31, 32]. For example, birds flock together to avoid predation [33], and ants locate foraging sites with seemingly random initial motion. At the same time non-cooperative behavior between predators and their prey is a fundamental activity in which animals engage [34]. Pursuit-evasion strategies that underlie such predator-prey interactions find strong interest in robotics and aerial navigation. In each case, mathematical models have greatly contributed to our understanding of the interaction rules that shape animal behavior. With advancements in data collection methods and new measurement tools, calibration of such models is now possible giving new insights into the physics of social interactions.

Citing examples of insect swarms and bird flocks, a critical issue in the quantification of collective animal behavior is addressed by Cavagna et al. [35], who investigate the main sources of error in three-dimensional reconstruction using a stereo camera setup. The authors perform a detailed analysis of trajectory accuracy of individual animals in such scenarios and perform precision tests, highlighting how to detect sources of inaccuracy. The authors analyze errors showing how to properly select camera setups that may be used in the design of three-dimensional experiments with collective animal behavior.

Rheotaxis is a behavior in which fish orient themselves relative to flow. Despite the fact that most species of fish school during at least some portion of their life, little is known about the importance of rheotactic behavior to schooling fish and, conversely, how the presence of nearby conspecifics affects rheotactic behavior. In their paper, Chicoli et al. [36] explore how group size and sensory noise affect schooling and rheotactic behavior. The authors propose a mathematical model in the form of a coupled-oscillator framework to model group rheotactic behavior. They further show that under noisy environmental conditions, increased group size improves rheotaxis.

In a multi-agent model of collective behavior, Gajamannage et al. [37] describe group motion as switching between low-dimensional embedding manifolds. They introduce a simple mapping for the agents between consecutive time-steps together with a novel metric of collective behavior, which encapsulates variations in the collective motion. The metric is successful in revealing the presence of distinct manifolds on which changes in collective behavior take place. Complementary to dimensionality-reduction techniques, this approach provides an effective model-free framework for the dynamic analysis of collective behavior.

Predatory dinoflagellates along with other microzooplankton consume about sixty percent of marine primary production, thus forming an important avenue for the transfer of carbon to higher trophic levels. In their work, Mazzoleni et al. [38] derive a simple model of dinoflagellate predator-prey system by drawing upon analogies from chemical kinetics. They modify their model to account for inefficiencies in predation. Simulation results are shown to match predictions and account for complex dynamics that were not included in the basic models; the results closely match the experimental observations thus reinforcing the notion that predatory dinoflagellates utilize toxins to increase their feeding rate. These findings lay the foundation for more predictive behavioral models of swimming behavior as a function of environmental variables and predation as a function of collision parameters.

In their paper, Ni and Ouellette [39] challenge existing definitions of collective behavior, which are typically associated with order in motion. They present and analyze insect swarms in a controlled laboratory setting, which though spatially disordered still exist as a collective. They measure the trajectories of each individual insect, and report negligible correlation. Their results, in contrast to long-range correlations found in wild swarms, point towards an alternate hypothesis: in a natural setting, insects may be independently responding in a similar way to some external stimulus, which would produce an apparent correlation in their behavior. The authors suggest new laboratory experiments to test this hypothesis where controlled external stimuli are intentionally introduced.

What are the determinants of social behavior and leader-follower relationships? These are open questions in animal dynamics that are also relevant in bio-inspired control of engineered multi-agent systems. In their work, Orange and Abaid [40] use an established model-free measure of causality to unravel interactions between flying bats. The authors study ten pairs of bats from a wild swarm navigating an environment near their roost and compute the transfer entropy between the curvatures of their flight paths. They find that a higher transfer entropy, meaning more information transfer, is computed from leading to following bats rather than from following to leading bats, which suggests that information propagates from front to rear bats as they fly in a group.

Pursuit and capture strategies in animals can inspire the navigation and control of unmanned aerial vehicles. In a review of the aerial prey capture dynamics in insects and bats, Pal [41] uses experimental data derived from literature to categorize prey pursuit and capture mechanisms into five different strategies. The author points out that established models of prey capture dynamics consider the pursuer and the prey as massless particles, and identifies possible future directions where detailed biomechanical models can be integrated with neural models of sensory input to expand the applications of pursuit and capture in bio-inspired design, navigation and control.

Strömbom et al. [42] study flocking behavior in moving animal groups using self-propelled particle models, in which traditional alignment-based rules are removed. The authors build on existing literature showing that models based on attraction only can generate a range of dynamic groups in two dimensional domains with periodic boundary conditions. By considering a weak global attraction term and by removing periodic boundary conditions, they show that there is no substantial difference between two and three-dimensional patterns of self-organization. Moreover, including repulsion results in the formation of global patterns that are consistent with characteristic collective features observed in animal groups.

Wongkaew and coauthors [43] utilize social balance theory proposed by F. Heider [44] to formulate a leadership-based optimal control problem with the purpose of driving a social network to attain a desired balanced state. Through numerical experiments, the authors demonstrate the ability of the proposed control strategy to drive the Heider balance model to friendship. The novelty of this work is manifold, since it

formulates and investigates a strategy to control (or stabilize) social networks in the sense of Heider. It is also interesting that this model focuses on the dynamics of the links-relationships that also enter as control functions.

Combining theoretical and experimental work, Zienkiewicz et al. [45] address the open question of how the underlying structure and dynamics of interactions between similar individuals allows for the emergence of leaders within the group. In particular, the authors propose a mathematical framework to capture the dynamics and interactions of small shoals of zebrafish, informed directly from experimental observations. They demonstrate how speed regulation can be leveraged to promote dynamical entrainment with an informed individual, and how the relative speed and interaction strength directly affects the degree to which an informed individual can a naive group.

## 4 Applied physics and robotics

Animals provide an everlasting resource of inspiration to physicists and engineers. Examples include bio-inspired and biomimetic systems for sensing and navigation, distributed algorithms for autonomous robots, novel tools of measurement and analysis that lead to a better understanding of the ecology and animal behavior, and the development of new materials inspired from the structure and function of animal parts [46–48].

Highlighting how the interaction between an animal and its environment may lead to novel solutions in engineering, Amador et al. [49] propose an alternative function to dense arrays of hairs observed throughout the compound eyes of insects, arising from their aerodynamics. After a thorough investigation comprising anatomical measurements using scanning electron microscopy, numerical fluid simulations, and wind tunnel experiments with insect eye mimics and at-scale micropillar arrays, the authors find that the hair arrays observed in 18 species of insects reduce airflow at the ocular surface by up to 90%. These results may motivate bio-inspired solutions for protecting sensitive surfaces, like lenses and sensors, from accumulating airborne debris, like dust and pollen.

Coral et al. [50] present a mathematical model for the free transverse vibration of a robotic fish, based on a continuous and non-uniform flexible backbone with distributed masses. The proposed approach is based on Timoshenko beam theory. The effects of the masses on the value of natural frequencies are investigated. Results are validated against analytical solutions available in the literature, and experiments on a physical prototype of a flexible fish backbone. The method allows the study of structures with nonuniform mass distributions and complex cross sections, which include realistic descriptions of biological systems and their biomimetic implementations.

Müller [51] investigates the dynamic properties of the horseshoe bat biosonar system that is characterized by an unusual dynamics at the interfaces between the animal and its environment. In particular, baffle structures in the biosonar system change their shapes to diffract the outgoing ultrasonic pulses and the returning echoes. The guiding hypothesis for this work is that the dynamics is key to encoding sensory information about structure-rich natural environments. Since navigating such environments still poses an insurmountable problem to engineered sensing solutions, insights into the dynamic sensory encoding in bat biosonar may have a transformative impact on the ability of man-made systems to operate in natural environments autonomously.

Timm-Davis and Fish [52] study flow dynamics within the nasal cavity of spiny dogfish using flow visualization techniques. In contrast with traditional assumptions on the morphology of the olfactory cavity, the authors demonstrate flow through the nasal apparatus and from the excurrent nostril to the mouth when respiratory flows

were simulated in dead animals. They find that the single nasal valve functions as an organization mechanism for the fluid, resulting in a coherent flow of water through the cavity. The results indicate that water could be drawn through the olfactory cavity via the morphology of the nasal apparatus and active swimming.

In the use of smart materials for biomimetic locomotion of robotic fish, Shahab and coauthors [53] explore the dependence of hydrodynamic thrust levels in macro-fiber composite actuators on the length-to-width aspect ratio. Using a non-linear semi-empirical Euler-Bernoulli-Morison model and Lighthill's theory to model the vibration response and experiments at various actuation voltage levels, the authors find that, while the inertia and drag coefficients are strongly dependent on the aspect ratio, resonant mean thrust to power consumption ratio is insensitive to this aspect ratio.

## 5 Open questions

Dynamics in animal systems fosters several broad areas of open research that demand attention from the scientific community. Five such open questions are highlighted here with the hope that they may inspire the curiosity of both experienced and junior researchers alike.

In light of the inherent inspiration that this work takes from biological systems, a first open question is how to build a stronger connection between mathematical models of animal dynamics and experimental data. Validating such models against noisy and sparse data from natural systems is a crucial step for which standard methods are often inadequate. A particularly elusive question entails the identification of model parameters that are involved in collective motions [54–61]. Since a particular instance of group coordination may result from a non-unique set of individual behaviors and interaction rules, how can we solve the inverse problem of determining model parameters? Simply put, when we observe a bird flock flying synchronously, how can we discover the rules that individuals use to attain those striking coordinated patterns?

Following up the idea of modeling an animal system, a second open question is to bridge the gap between highly refined physical models, minimalistic lumped parameters models, and practical experimentation [62–67]. This translational work is necessary to allow modeling efforts to become cogent tools for empirical studies on animal systems. While biological systems are often over-actuated and over-sensorized, such detail in physical models could be unnecessary and impractical for the goal of understanding a biological system. With that in mind, how do we determine the salient variables for reduced-order modeling in the context of a given research question?

From an experimental perspective, a third open question is how to devise high throughput techniques for calibrating models and validating key hypothesis on animal dynamics, such as their locomotion, sensing, or social behavior [68–74]. Currently, ethograms of animal behavior are often constructed around a sequence of observer-driven data analysis steps, which are both time-intensive and subjective to observer training and bias. Since large scale model validation will rely on ethograms based on both temporally and spatially resolved data sets, how can we achieve sufficient technological advances in data collection and processing?

Beyond purely observational approaches, a fourth open question focuses on using biologically-inspired robotics to better understand the dynamics of animal systems. While significant efforts have been devoted to such robots, the range of applications is primarily human-centered. Specifically, a wide range of robots is currently being developed based on their animal counterparts, yet these robots are seldom used to interact with animals. We posit that such robots may offer a unique opportunity to

influence animal behavior and design new hypothesis-driven experiments in which we could precisely isolate desired independent variables [75–86]. For example, if we were interested in understanding the role of body size on fish social behavior, we could engineer an array of robots that are identical in their morphology and locomotion, and systematically vary their size. By studying the response of live fish to such robots, we could precisely isolate the role of the body size as an independent variable. In more general terms, how can we use these incredible technological advancements to better understand the dynamics of animals?

Comparing animal systems across species and physical scales, a fifth open question deals with universality classes and scaling laws in animal physiology, behavior, and sociality. While much data may be collected and conclusions drawn about isolated animal systems, a way to relate these results across systems is currently lacking. We can all appreciate similarities between human crowds and ant colonies or fish schools, yet a physically-grounded rigorous approach to abstract the key features of animal dynamics is currently not available. Dimensionality reduction techniques have been proposed as a valuable tool to shed light on such similarities in the context of collective behavior [87–91], but the state of the art still lacks of a robust theoretical basis to systematically abstract, without human intervention, common features of animal dynamics across different phyla of life. How can we identify invariant aspects of animal systems to enable the development of unifying theories governing the dynamics of such systems?

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