



SYMPOSIUM INTRODUCTION

Mechanoethology: The Physical Mechanisms of Behavior

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Synopsis Research that integrates animal behavior theory with mechanics—including biomechanics, physiology, and functional morphology—can reveal how organisms accomplish tasks crucial to their fitness. Despite the insights that can be gained from this interdisciplinary approach, biomechanics commonly neglects a behavioral context and behavioral research generally does not consider mechanics. Here, we aim to encourage the study of “mechanoethology,” an area of investigation intended to encompass integrative studies of mechanics and behavior. Using examples from the literature, including papers in this issue, we show how these fields can influence each other in three ways: (1) the energy required to execute behaviors is driven by the kinematics of movement, and mechanistic studies of movement can benefit from consideration of its behavioral context; (2) mechanics sets physical limits on what behaviors organisms execute, while behavior influences ecological and evolutionary limits on mechanical systems; and (3) sensory behavior is underlain by the mechanics of sensory structures, and sensory systems guide whole-organism movement. These core concepts offer a foundation for mechanoethology research. However, future studies focused on merging behavior and mechanics may reveal other ways by which these fields are linked, leading to further insights in integrative organismal biology.

Introduction

A central question in organismal biology is: how do organisms accomplish the tasks they face? How does a predatory fish successfully capture evasive prey, and how does the prey avoid capture? How does a male bird defend its territory from conspecific competitors and, later, attract a female mate? One way to answer this central question involves linking behavior—describing the tasks organisms face—with its underlying physical mechanisms, or mechanics—quantifying the movements and forces organisms, and their environments, exert when executing tasks.

The fields of behavior and mechanics have been connected, explicitly or implicitly, for decades. For example, Tinbergen, in his seminal “Four Questions” paper (1963), equated behavior with movement when he defined Ethology as “... ‘the biological study of behaviour’

... characterized by an observable phenomenon (behaviour, or movement)...” From the mechanics side, Koehl (1996) defined biomechanics as the application of engineering techniques to understand how organisms perform functions, including movement. These examples and others (e.g., Garland and Losos 1994; Lauder 1995; Lailvaux and Husak 2014) make clear the importance of integrating research in mechanics with research in behavior. However, despite repeated calls for the broader use of this cross-disciplinary approach (e.g., Byers et al. 2010; Briffa and Lane 2017; Rico-Guevara and Hume 2019), studies of the mechanics of behavior are rare. This may be because, for example, behaviorists have little background with the tools of mechanics research, while those studying mechanics are inexperienced in linking their findings with broader behavioral theories or principles (Losos et al. 2002; Careau and Garland 2012).

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Here, we introduce “mechanoethology” as a term intended to encompass research integrating behavior and mechanics. As we detail in examples below, a mechanoethology approach uses techniques from mechanics research (e.g., biomechanics, physiology, functional morphology) to address questions related to, or inspired by, behavioral theory (e.g., sexual selection, collective behavior). Therefore, in addressing the question of how organisms accomplish the tasks they face, mechanoethology research integrates the behavioral theory of *why* organisms undertake those tasks with the biomechanical, physiological, and morphological mechanisms that describe *how* organisms execute those tasks.

This framework is distinct from similar perspectives in its scope of both behavior and mechanics. For example, while [Garland and Losos \(1994\)](#) usefully introduced “behavior” into the classic “morphology → performance → fitness” framework of [Arnold \(1983\)](#), they used behavior as a way to capture how an organism’s performance (usually measured as a maximum value in the lab) is realized in natural interactions (similar to the “realized niche” of [Wainwright 1991](#)). Mechanoethology is more specific in suggesting how behavioral *theory* can lead to specific predictions about, among other topics, performance and morphology. These predictions can be tested using mechanics techniques. In a similar vein, the recently introduced field of “mechanical ecology” ([Bauer et al. 2020](#)) usefully calls for more field-based approaches to organismal biomechanics. Mechanoethology is distinct in both a broader focus on mechanics writ large (including, e.g., physiology and functional morphology) and a more constrained focus on behavior as opposed to ecology. We note that, while we tend to focus on connections to animal behavior, mechanoethology can extend to nonanimal taxa, including plants (e.g., [Crofts and Stankowich 2021](#)).

Core concepts in mechanoethology

Integrating behavior and mechanics can benefit research in both fields. [Table 1](#) lists core concepts in mechanoethology, showing how research in one field can influence the other. We broadly describe these concepts in this section, referencing later sections in this Introduction and papers in this issue that give more detailed examples.

Energy is a central currency in both behavior and mechanics. Much animal behavior research is based on building and testing theories related to the costs and benefits of specific movements ([Rubenstein and Alcock 2018](#); [Dugatkin and Reeve 2000](#)). While these costs and benefits ultimately affect fitness (e.g., number of surviving offspring), measurements of energy may serve

as a proxy for fitness and a link to the mechanics of behavior. The fact that any behavior requires energy, and that energetics is driven by mechanics, means that mechanics sets the energetic costs of behavior. Further, mechanics techniques offer approaches to measuring energy use (e.g., through kinematics or force output). In the “Collective behavior” section, below, we describe how biomechanical studies measuring the energetics of fish swimming help quantify the relative costs and benefits of schooling behavior. From the mechanics perspective, any mechanistic study of the energetics of movement should start by understanding the behavioral context of that movement. If animals are under selection to balance the energetic costs and benefits of their movements (i.e., their behaviors), then mechanistic studies of these movements, and the structures that produce them, are most valid when couched in the appropriate behavioral context. [Sargent et al. \(2021\)](#) contextualize studies on aerodynamics and energetics of hummingbirds with seemingly opposed behavioral strategies, namely stationary interference and traveling exploitation. Also in this lens of mechanoethology, [Rico-Guevara et al. \(2021\)](#) connect hummingbird bill morphology with the energetic costs and benefits of foraging on flowers with different morphologies, all while considering hummingbird behavior, ecology, and evolution.

Mechanics and behavior also provide each other with important limits and, sometimes, ways to bend or break those limits. Any behavior is constrained by its underlying mechanics. For example, force–velocity trade-offs in muscle physiology mean that muscle contractile force is inherently linked to, and therefore limited by, contractile velocity ([Longo et al. 2019](#)). These physical limits mean that some behaviors, no matter how “adaptive” they *could* be, might simply be physically impossible. However, mechanical innovation may provide ways to overcome these limits and expand behavioral boundaries. The section “Animal communication” details studies in golden-collared manakins in which the limits of muscle physiology are stretched, connecting to the evolution of dynamic display behaviors. The limits imposed on mechanics by behavior are not physical, but ecological and/or evolutionary. Any physical mechanism will be influenced, and limited, by the ecology and evolutionary history of the organism(s) involved (e.g., [Gould and Lewontin 1979](#); [Wainwright 1991](#)). Ecological and evolutionary boundaries may also be broad, however. For example, some structures are multifunctional, being used for multiple behaviors. This multifunctionality arises because animals evolve new ways of using existing structures (e.g., exaptation, [Gould and Vrba 1982](#)). Any study of mechanism should ground itself in the ecological and evolutionary boundaries rele-

Table 1 Core concepts in mechanoethology. For each concept, we list what insights mechanics can provide behavior and what insights behavior can provide mechanics

Concept	What mechanics provides behavior	What behavior provides mechanics	Examples
Energy	Mechanics sets the energetic cost of motion.	Behavior provides the context and budgeting of energy use.	Schooling fish (Herskin and Steffensen 1998). Hummingbird bills (Rico-Guevara et al. 2021).
Limits	Mechanics imposes physical limits on behavior. Physical limits can be expanded through mechanical innovation.	Behavior contributes ecological and evolutionary limits to mechanical systems. Limits can be broadened by multifunctionality and behavioral innovation.	Displaying manakins (Barske et al. 2014). Defensive spines (Crofts and Stankowich 2021). “Enhancers,” including springs (Higham and Irschick 2013; Longo et al. 2019). Hummingbird bills (Rico-Guevara and Araya-Salas 2015).
Sensation	Behavioral sensation is underlain by the mechanics of sensory structures.	Sensory behavioral responses form the impetus for and feedback during movement.	Fish predator–prey interactions (Peterson et al. 2021). Competing mantis shrimp (Green et al. 2019; deVries et al. 2021).

vant to that mechanism (and often studied via behavioral approaches). Crofts and Stankowich (2021) describe the ecological and evolutionary forces underlying defensive spine morphology and biomechanics, and the section “Intrsexually selected weaponry” in this Introduction shows how mechanoethology approaches revealed multifunctionality in hummingbird bills (see also Rico-Guevara and Araya-Salas 2015).

Finally, sensation is a key concept in both mechanics and behavior. All organismal behaviors require sensation; for example, a prey cannot avoid a predator without sensing it first. Sensation is inherently a mechanical process, as sensory structures must move to engender a sensory response (e.g., the bending of mechanosensory hairs leads to action potentials). Behavioral studies that consider the mechanics of sensation can find new insights that did not arise without this perspective. The section “Animal communication” and deVries et al. (2021) describe the behavior and mechanics of ritualized striking in mantis shrimp, suggesting how the sensation of strike energy might influence contest behavior. From the mechanics side, any mechanistic study of movement should recognize that the movement came in response to some sensed stimulus (including feedback-based sensation of an organism’s own movement). For example, the movements of both predator and prey in fish predator–prey interactions can be better understood when considering how each party senses the other (Peterson et al. 2021).

Examples of mechanoethology

In this section, we detail examples from the literature in which mechanoethology approaches have lent insight to both behavior and mechanics research.

Animal communication

Interacting animals often communicate using signals. For example, male jumping spiders court prospective female mates by displaying color patches (visual signals), waving their legs above their heads (movement-based signals), and drumming their abdomens and legs on the ground (acoustic/vibrational signals) (Echeverri et al. 2017). Female receivers of signals like these are thought to use them to assess a male’s quality and decide whether or not to mate with him (e.g., Brandt et al. 2020). Like those of male jumping spiders, other signals—from acoustic, to chemical, to movement-based—are used by receivers to gather information on the signaler or the environment (Seyfarth et al. 2010). Major questions in animal communication include: what are the mechanics of signal production, and what information do receivers of signals gather from those signals? Mechanoethology approaches have helped develop answers to these questions.

Competing individuals are thought to exchange signals that, through energetic costs, help opponents assess their own and/or their competitor’s ability and decide to give up or stay in the fight (reviewed in, e.g., Searcy and Nowicki 2005). Recent work has shown how mechanics approaches can be used to quantify the energetic costs of these signals, helping behaviorists understand signal assessment. During contests, mantis shrimp (*Neogonodactylus bredini*) ritualistically exchange high-force strikes, delivered by weaponized raptorial appendages onto each other’s armored tailplates in a behavior called “telson sparring” (Green and Patek 2015; Fig. 1A). This sparring serves a communicative function, helping individuals assess relative competitive ability (of which body size is a proxy) and decide to give up a contest instead of simply inflicting

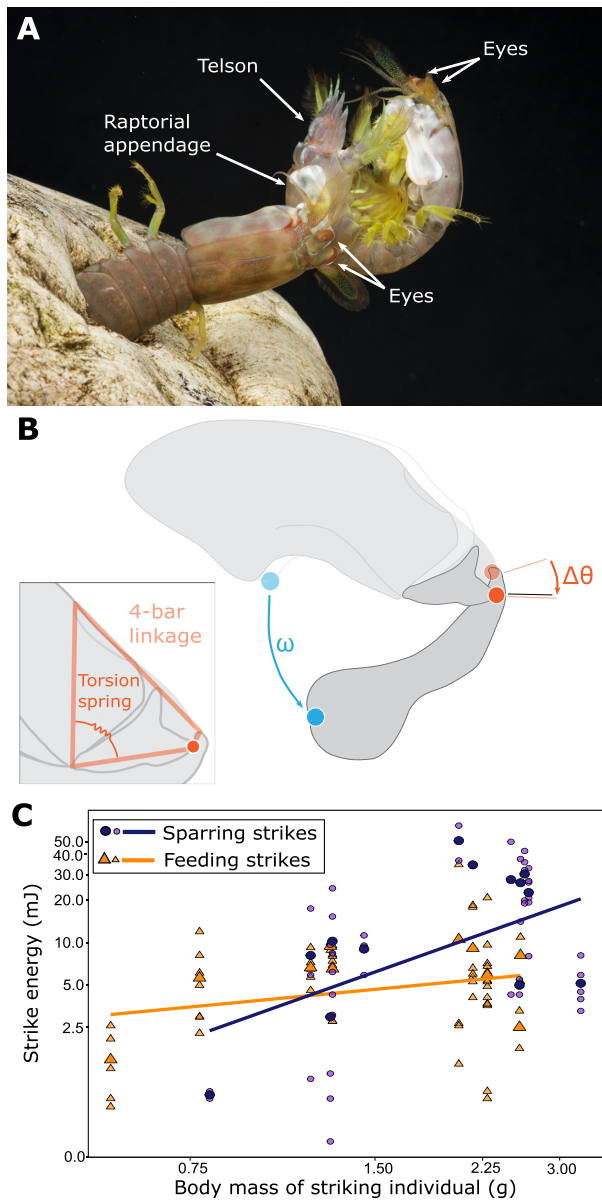


Fig. 1 (A) A mantis shrimp (left) delivering a raptorial appendage strike onto its competitor's (right) coiled telson. (B) Biomechanical modeling of the strike mechanism showed that the energy used to power a strike can be quantified by measuring strike velocity ($\frac{\Delta\omega}{\text{time}}$). The energy is stored and released from a torsion spring (inset), which is part of a four-bar linkage system (inset) that displaces (θ) to actuate the strike movement. (C) Calculating strike energy from the velocity of strikes recorded using high-speed video showed that strike energy increased with increasing body size for sparring strikes (purple), but not feeding strikes (orange). Figures adapted from Green et al. (2019).

damage (Green and Patek 2018). While behaviorists knew that sparring helped competitors gather information about each other, an open question remained: what information is communicated during sparring? That is, what can an individual receiving a strike assess about its competitor? This question was answered with

the help of the long history of biomechanics work in mantis shrimp. Earlier studies of mantis shrimp strike biomechanics revealed that an exoskeletal spring stores and releases the energy of the strike (reviewed in Patek 2019). This work led to mathematical models that could quantify the energy required to deliver a strike, given the velocity of the strike and the mass of the striking appendage (McHenry et al. 2012, 2016; Fig. 1B). Green et al. (2019) applied this biomechanics work to quantify the energy of telson sparring strikes. They measured strike velocity from high-speed videos of freely competing mantis shrimp and combined this with measures of competitor appendage mass, incorporating both into the biomechanical model to calculate strike energy. This approach revealed that larger mantis shrimp delivered higher energy sparring strikes than smaller mantis shrimp, a positive scaling not seen when mantis shrimp used their strikes on prey items (snails; Fig. 1C). Because this positive scaling of energy with body size was unique to sparring, and because body size is a proxy of competitive ability (Green and Patek 2018), Green et al. (2019) suggested that, during sparring, mantis shrimp strike energy communicates the striking individual's size and, therefore, its ability. The natural history of mantis shrimp supports this hypothesis. Mantis shrimp live in (and compete over) dark burrows in coral rubble (e.g., Green and Harrison 2020), meaning competitor body size is often hard to assess visually. Sparring might be an efficient means of gathering body size information that would otherwise be hidden. While the physical mechanism by which the receivers of strikes sense strike energy is still unknown, the surfaces of other animal structures used to receive competitive forces have high densities of mechanoreceptors (e.g., stag beetle jaws, Goyens et al. 2015; rhinoceros beetle horns, McCullough and Zinna 2013). Mantis shrimp telsons may similarly have structures that allow for sensation of strike energy (through, e.g., strike force).

Research on mate choice in birds shows how a mechanoethology approach can reveal the energetics of and mechanical limits on animal behavior, as well as how animals stretch mechanical boundaries. Male golden collared manakins produce dynamic signals toward females who are choosing among prospective mates. These signals involve males jumping acrobatically from perch to perch and, while jumping, snapping their wings above their heads to produce sound (a wingsnap; see Clark 2021, this issue, for a discussion of wing-based sound production). Barske et al. (2011) found males that wingsnap more frequently have higher mating success. Further, using high-speed video recordings of signaling behaviors, they found that sub-second differences in male choreography influence fe-

male choice. This basic knowledge of the importance of dynamic signaling to mating success led to further questions at the intersection of behavior and mechanics: how costly are these signals, and what physical mechanisms underlie their performance? The first question was answered when Barske et al. (2014) calibrated manakin heart rate with oxygen metabolism-based measures of energy use in the lab. By measuring heart rates of signaling males in the field, the researchers could infer the metabolic costs of signaling from their prior calibration. This clever approach revealed that manakin signals—which increased heart rate to over 1000 bpm—required a remarkable 5.5 kJ/h of energy! This energy expenditure could be prohibitive, but field-based behavioral observations showed that signals last approximately 10 s each, and, on average, manakins signal for only 5 min per day. The result is an average cost of only 1.2% of a manakin's daily energy budget. Therefore, while signals are instantaneously costly, their long-term costs are quite manageable. Later work using classic muscle physiology approaches revealed that golden collared manakins have evolved superfast muscle contractile physiology to produce such acrobatic signals. Fuxjager et al. (2016) electrically stimulated dissected wing muscles of golden collared manakins, and those of related species, at frequencies similar to those required to produce repeated wingsnaps. By measuring the force outputs of these repeatedly stimulated muscles, they found that the muscle used to produce wingsnaps was able to relax nearly fully, and therefore to remain functional, even over the fast frequencies of stimulation required to produce wingsnaps. In comparison, the same muscles in species that do not produce wingsnaps showed no such ability; neither did other muscles used in flight, but not in signaling, in all species (Fuxjager et al. 2016). This analysis—using techniques most physiologists learn in undergraduate studies—revealed how the limits of muscle force–velocity tradeoffs are stretched in animals that have evolved dynamic, fast signals.

Introsexually selected weaponry

The previous examples presented approaches that began with a behavioral observation that led to behavioral hypotheses to be tested through mechanistic approaches. In contrast, in this section we will present a case study that starts with the discovery of sexually dimorphic morphology that did not conform with previous ecological explanations, and the experimental journey to identify its secondary function as an introsexually selected weapon (ISW). The definition of ISWs, on its own, includes a combination of behavior and morphology linked to a mechanism (Rico-Guevara and Hurme 2019). A trait can be considered an ISW

if it (1) is used as a weapon during same-sex agonistic encounters and (2) is only present or enlarged (relative to body size) in one of the sexes. The concept of ISWs thus goes beyond assumptions of exaggerated sexually dimorphic traits that resemble weapon-like structures but have little behavioral evidence of being used as weapons (e.g., Fig. 4 in Emlen 2008); hence, it is stricter regarding the behavioral evidence of structures actually used as weapons. It also subsumes other widely used terms (e.g., sexually selected weapons, sexually dimorphic weapons, see for instance Rico-Guevara and Araya-Salas 2015) whose definitions do not encompass all ISWs (reviewed in Rico-Guevara and Hurme 2019). For example, sexually selected weapons are defined as traits used in direct fights between individuals of the same sex over access to individuals of the opposite sex for mating purposes (Berglund 2013); this has as a prerequisite the idea that same-sex fights are over access to mates. The definition of ISWs does not have such prerequisite, making it applicable to cases such as the weaponry of female dung beetles (Emlen et al. 2005), which fight among themselves for dung balls as opposed to battling over males. Another advantage of the term ISWs over other related, widely used terms (e.g., sexually selected weapons, sexually dimorphic weapons) is that it explicitly specifies the kind of sexual selection under which the weapon evolved: intrasexual selection. Other sexually dimorphic weapons have evolved through natural selection (e.g., enlarged mandibles in female soldier ants; Molet et al. 2012); still others under different selective pressures related to sexual selection (e.g., weapons used in sexual coercion; Stutt and Siva-Jothy 2001). These, and other examples (Rico-Guevara and Hurme 2019), show the importance of relying on behavioral approaches instead of inferring a structure's function based purely on morphological differences between the sexes. Below, we present a case study that uses both behavior and mechanics approaches to test for the existence of ISWs. We conclude the section with a roadmap of the behavioral determinants for the evolution of ISWs.

The long-billed hermit (*Phaethornis longirostris*) is a hummingbird that has a bill shape sexual dimorphism in length and curvature that had previously been linked to differences in floral resource exploitation between males and females (Temeles et al. 2010). However, Rico-Guevara and Araya-Salas (2015) found dagger-like bill tips in males that were challenging to explain under the ecological causation hypothesis (Temeles et al. 2000, 2010). An alternative explanation for sexually dimorphic traits, even when found in feeding structures (see Rico-Guevara and Hurme 2019), is that they could serve in combat. Rico-Guevara and Araya-Salas (2015) established four predictions that required approaches from

both mechanics and behavior to test: (1) the trait is enlarged or only present in one of the sexes (morphology), (2) it appears or enlarges during puberty (development), (3) it is suited to inflict damage during fights (biomechanics), and (4) weaponized males exhibit elevated dominance status (they have a fighting advantage) that is linked to mating success (behavior). The first two predictions would confirm that the trait is a secondary sexual trait (see Venn diagram in Rico-Guevara and Hurme 2019) and the last two would corroborate the trait as an ISW, providing an explicit hypothesis for its evolution as a weapon. Through a morphological survey using macrophotography on both museum and live specimens, Rico-Guevara and Araya-Salas (2015) found that adult male *P. longirostris* had pointier and elongated (dagger-like) maxillary overhangs that were absent in females and juveniles, supporting the two first predictions outlined above. Then, the authors assessed if male bills were more suitable to inflict damage when compared to female and juvenile bills, which present bill tips similar to the ones of most other hummingbirds (Rico-Guevara and Rubega 2017). Using a setup designed to measure the force required for a bill to perforate an experimental film, it was shown that *P. longirostris* males with enlarged and pointier bill tips had greater puncture capabilities (i.e., required less force to puncture the film), which would potentially confer a fighting advantage (Rico-Guevara and Araya-Salas 2015). Long-billed hermits are lek breeders: lekking males fiercely defend the perches from where they sing to attract females (Stiles and Wolf 1979). Rico-Guevara and Araya-Salas (2015) recorded agonistic behaviors and captured on video how males stabbed each other with their sexually dimorphic bill tips (also found in other spp., Rico-Guevara et al. 2019). In addition, by using territory mapping and mark-recapture techniques in 5 leks and during 4 years, they demonstrated that males with enlarged and pointier bill tips were more successful in defending lek territories. This final link is suggestive of a relationship between increased fitness and developed weaponry; in other lek breeders, males that defend leks more successfully sire most of the next generation (Balmford et al. 1992; Rintamäki et al. 2001; Isvaran 2021). However, further research has shown that other phenotypic traits are also important to consider when studying the success of these lek breeders (e.g., cognition, Araya-Salas et al. 2018).

Using a mechanoethology approach, all four predictions for these bills to be ISWs were fulfilled. This new ISWs perspective provides an alternative explanation to ecological causation for the origins of sexual dimorphism in hummingbird bills that ought to be explored through future comparative and experimental approaches. For example, sexual dimorphism in bill

length and curvature has been attributed to intersexual niche partitioning (Temeles et al. 2000, 2010), yet Rico-Guevara and Araya-Salas (2015) also found that both curvature and pointiness partially explained the lower force adult males need for piercing. Male *P. longirostris* have overall longer and straighter bills than females (Stiles and Wolf 1979; Temeles et al. 2010), additionally, juvenile males transitioned from curved to straighter bills and acquired longer bill tips during puberty (Rico-Guevara and Araya-Salas 2015). Elongated structures are mechanically more resistant to buckling, during axial loading, when they are straighter (e.g., Dahlberg 2004). Hence, longer bills can confer an advantage during bill-sparring through increased reach (same rationale of the “pommeling” technique in fencing), and a straighter bill would be able to transmit more force to the tip resulting in elevated potential damage to an opponent. Lastly, Rico-Guevara and Araya-Salas (2015) found that *P. longirostris* males have thicker bills, potentially better at resisting bending forces when stabbing. Salient questions in this regard include: Do ecological causation and the “bills as ISWs hypothesis” predict the same directionality and kind of sexual dimorphism? Could coevolution between bill shape and flower shape boost underlying sexually dimorphic patterns resulting from a different selective force (e.g., favoring bills as ISWs)? Are ISWs in hummingbird bills also favored by natural selection (via interference competition), are they in opposition to it (via trade-offs with nectar intake efficiency), or both?

Collective behavior

The study of collective animal behavior aims to understand how the interactions among individuals in a group yield emergent properties for the group (Sumpter 2010). In a number of respects, an animal collective offers more than the sum of its parts, with a capacity for memory, responses to stimuli, and cognitive processing that exceed the abilities of an individual (Sosna et al. 2019). Collective behavior emerges from communication between animals and can be influenced by forces transmitted between them. In fish schools, fluid dynamics offer both a source of information transmission (“Sensation” in Table 1) as well as the means for individuals to influence the propulsion generated by conspecifics, with energetic implications (“Energetics” in Table 1). Schooling consequently offers a system for the study of mechanoethology where behavior both affects, and is affected by, mechanics in multiple respects.

It has long been recognized that fish may swim at a reduced energetic cost when moving in a school (Breder 1926, 1965). This idea is most readily supported by measurements of tail-beat frequency. Tail-beat frequency

is tightly correlated with swimming speed in solitary fish (Bainbridge 1958) and the energetic cost of swimming varies with the square or cube of tail-beat frequency (Herskin and Steffensen 1998; Steinhausen et al. 2005). It is therefore energetically meaningful that fish in a school can attain the same speed at a lower frequency than when swimming solitary. For example, a tetra (*Hemigrammus bleheri*) swims at a rapid speed (4 body-lengths/s) with a tail-beat frequency of ~ 10 Hz in a school, but requires a frequency of ~ 17 Hz to attain the same speed when alone (Ashraf et al. 2017). Similar effects have been observed in mullet (*Liza aurata*; Marras et al. 2015), the intermittent swimming of shiners (*Notemigonus crysoleucas*; Fish et al. 1991), and the pectoral-fin swimming of surfperch (*Embiotoca lateralis*; Johansen et al. 2010). Given the nonlinear relationship with energetic cost, these reductions in frequency have the potential to yield disproportionately large energetic savings (Herskin and Steffensen 1998). However, behaviorists have pointed out that these results should be regarded with caution because metabolic rate is also dependent on the stress level of an animal, and schooling fish are less stressed when surrounded by conspecifics (Nadler et al. 2016). Therefore, an understanding of hydrodynamics is necessary to parse the mechanical benefits of this collective behavior from the confounding influence of reduced stress (Li et al. 2020).

Hydrodynamic interactions between fish have the potential to enhance thrust production and the efficiency of swimming. Undulatory swimming is characterized by the shedding of a vortex at the lateral excursion of each half tail-beat (Rosen 1959). As a consequence, the wake behind a fish features a series of vortices, each of which resembles a smoke ring of swirling flow with a jet at its center (Fig. 2A). Weihs (1973) suggested that a fish that trails others may benefit by positioning itself between these vortices, where induced flow velocities could be directed in the swimming direction (Fig. 2B). It was predicted that a diamond-shaped arrangement of fish in the school achieves this aim. He additionally proposed that neighboring fish may enhance thrust by channeling flow between their two bodies. In subsequent studies, the diamond pattern has generally not been shown to be exhibited by fish (Partridge and Pitcher 1979; Marras et al. 2015; Ashraf et al. 2017), but it is clear that schooling fish can benefit from hydrodynamic interactions when they swim closely together.

A number of recent studies have offered an explicit consideration of the fluid dynamics of interacting fish bodies, principally through computational fluid dynamics and fish-inspired robots. These approaches consider much of the complexity of deforming bodies in flow that were not possible in Weihs' (1973) era, includ-

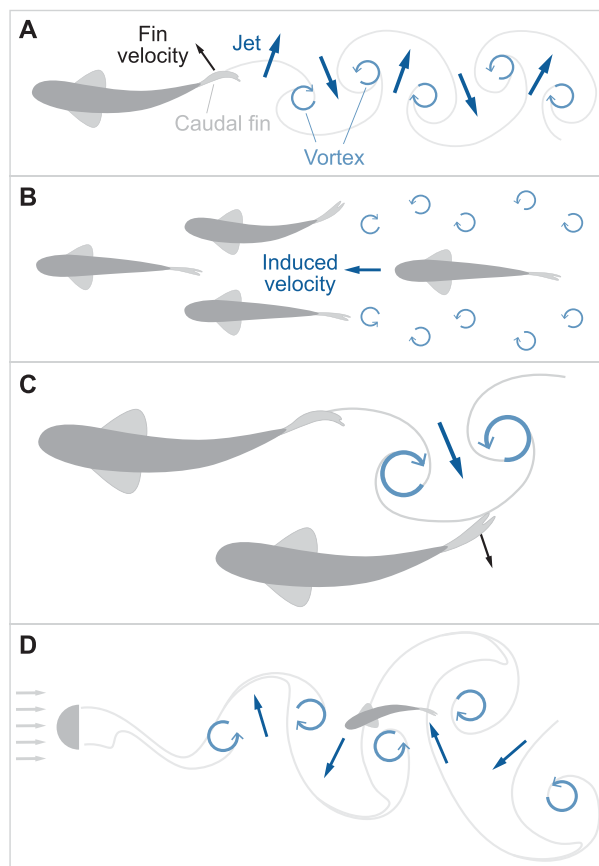


Fig. 2 Hydrodynamic mechanisms of enhancing thrust in a wake. **(A)** Thrust generation of a swimming fish includes the shedding of a series of vortices (Rosen 1959). Each vortex features a jet that is directed laterally and in the direction of thrust. **(B)** Weihs (1973) proposed that vortices in the wake between neighboring fish may induce flow in the direction of swimming that could benefit the thrust generated by a trailing fish, a mechanism suggested to work for fish swimming in a diamond-shaped arrangement. **(C)** Vortex phase-matching occurs when a trailing fish coordinates its tail beating relative to the vortices shed by a leading fish to enhance propulsion (Li et al. 2020). **(D)** Trout exhibit a Kármán gait when swimming in the wake of a semicylinder (Liao et al. 2003a). The fish successfully holds station at a relatively low frequency by slaloming between shed vortices.

ing three-dimensional effects, turbulence, and viscous dissipation. This work demonstrates that it is possible for fish to swim more efficiently in a school of seemingly any spatial arrangement. Arrangements in a diamond pattern, aligned in series, side-by-side (i.e., a phalanx), and a square formation can offer energetic savings over solitary swimming (Daghooghi and Borazjani 2015; Hemelrijk et al. 2015; Maertens et al. 2017; Verma et al. 2018; Li et al. 2019a, 2019b; Lin et al. 2019). The manner in which these benefits arise depends on the proximity between the fish; the relative timing of tail beating can also be important. For example, based on measurements from robotic fish, Li et al. (2020) pro-

posed the mechanism of vortex phase-matching. This requires that a follower fish shed vortices with a delay after the leader fish's such that the jets of the two vortices sum by pointing in a similar direction (Fig. 2C). The tail-beat phase that achieves this depends on the speed of swimming and the relative position of the follower.

A behavioral approach offers the promise of determining whether fish take advantage of the hydrodynamic benefits to schooling. Liao et al. (2003a) made the exciting discovery that trout (*Oncorhynchus mykiss*) adopt a novel gait when holding station in the wake behind a semicylinder (Fig. 2D). This Kármán gait is characterized by swimming at a reduced tail-beat frequency as the fish slaloms between the vortices shed by the cylinder (Liao et al. 2003b). The wake behind a bluff body is different from that of a swimming fish (Fig. 2), but these experiments demonstrate an ability of a fish to position itself and alter its swimming kinematics to take advantage of the vortices within a wake. Based on a kinematic analysis of station-holding by a school, both goldfish (*Carassius auratus*; Li et al. 2020) and tetras (*H. bleheri*; Ashraf et al. 2016) exhibit periods of swimming that are either in-phase with close neighbors, or slightly phase-shifted. However, Li et al. (2020) estimated that goldfish coordinate their swimming with neighbors often enough to realize only about 15% of the total energetic savings possible from vortex phase-matching. Therefore, fishes do coordinate their spacing and timing of swimming to realize energetic gains, but these may not be dominant factors in routine swimming behavior. One might expect energetic economy to be of greatest importance in species that migrate long distances and/or station-hold under intense flow speeds, but it remains to be seen if fishes under these conditions seek energetic savings with greater frequency. Under these conditions, hydrodynamics may offer an explanation for the limits to the speed and energetic costs of swimming in a school ("Limits" in Table 1).

Fluid flow may be sensed by group members, thereby serving as a source of information to facilitate collective behavior. Fishes have a capacity to sense water flow, which can supplement visual cues to regulate the spacing between the members of a collective. The fish lateral line system includes two types of flow receptors. Superficial neuromasts project from the skin, where they encode the velocity of flow at the body's surface. Canal neuromasts reside within bony canals that have pores at the surface, which allow for the sensing of flow acceleration (van Netten and Kroese 1989; Kroese and Schellart 1992; van Netten and McHenry 2013). Partridge and Pitcher found that individual saithe (i.e., pollack, *Pollachius pollachius*) remain capable of schooling when blinded, but only if the lateral line is fully func-

tional (Pitcher et al. 1976; Pitcher 1979; Partridge and Pitcher 1980). These findings suggest that both the visual and lateral line systems are sufficient for schooling. However, flow sensing has been shown to be insufficient for schooling in a diversity of fishes that fail to maintain a school in the dark, including cyprinids (*Danio rerio*; Schulze et al. 2018), mackerel (*Scomber scombrus*; Hunter 1968), juvenile tuna (*Thunnus orientalis*; Torisawa et al. 2007), juvenile salmon (Ali 2001), and tetras (*Hemigrammus rhodostomus*; McKee et al. 2020). By experimentally compromising the lateral line, a number of studies have demonstrated alterations in the spacing and polarization of schooling fish (e.g., Partridge and Pitcher 1980; Mekdara et al. 2018; McKee et al. 2020). Therefore, the lateral line aids in navigating with respect to neighboring fish, but has largely been shown to be insufficient to maintain a cohesive school.

Birds that fly in formation are potentially capable of realizing energetic benefits to flight in a manner similar to schooling fish. For example, great white pelicans (*Pelecanus onocrotalus*) fly at a reduced heart rate when in formation compared to flying at the same speed on their own (Weimerskirch et al. 2001). A gliding bird, or fixed-wing aircraft, sheds vortices at its wing tip. This swirling flow induces downward flow behind the flier and upward flow (i.e., "upwash") at positions to the left and right of the wings. Upwash presents an opportunity for a trailing bird to enhance lift generation with flow that is induced by a leading bird, but this requires precise positioning. By GPS tracking individuals, Portugal et al. (2014) demonstrated that northern bald ibises (*Geronticus eremita*) flying in a "V" formation regulate their position to capitalize on the upwash generated by leading birds. In addition, follower birds flap their wings with a delay that follows the wing motion of leaders to track undulations in position of the wing-tip vortices. It is unclear how this coordination is achieved, but bird wings do possess an arrangement of mechanoreceptors that could sense airflow over the wing's surface (Hörster 1990; Brown and Fedde 1993) and thereby supplement visual cues in a manner analogous to the role played by the lateral line in fishes.

Conclusion

Integrating behavioral theory with principles and approaches from mechanics can lend new insights to our understanding of how organisms accomplish crucial tasks. We have identified energy, limits, and sensation as key concepts in mechanoethology (Table 1). However, it is likely that there are other ways in which the fields of behavior and mechanics contribute to each other. The other papers in this special issue show how approaches that connect physical mechanisms and behavior can be

used to understand topics as diverse as reproduction (Brennan et al. 2021; Johnson et al. 2021), competition (deVries et al. 2021), foraging and avoiding predation (Crofts and Stankowich 2021; Peterson et al. 2021; Rico-Guevara et al. 2021), and communication (Clark 2021). We encourage future studies that further reveal the intersectionality between animal behavior and its underlying mechanics.

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