The Company of **Biologists**

COMMENTARY

Energetics of collective movement in vertebrates

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ABSTRACT

The collective directional movement of animals occurs over both short distances and longer migrations, and is a critical aspect of feeding, reproduction and the ecology of many species. Despite the implications of collective motion for lifetime fitness, we know remarkably little about its energetics. It is commonly thought that collective animal motion saves energy: moving alone against fluid flow is expected to be more energetically expensive than moving in a group. Energetic conservation resulting from collective movement is most often inferred from kinematic metrics or from computational models. However, the direct measurement of total metabolic energy savings during collective motion compared with solitary movement over a range of speeds has yet to be documented. In particular, longer duration and higher speed collective motion must involve both aerobic and non-aerobic (high-energy phosphate stores and substrate-level phosphorylation) metabolic energy contributions, and yet no study to date has quantified both types of metabolic contribution in comparison to locomotion by solitary individuals. There are multiple challenging questions regarding the energetics of collective motion in aquatic, aerial and terrestrial environments that remain to be answered. We focus on aquatic locomotion as a model system to demonstrate that understanding the energetics and total cost of collective movement requires the integration of biomechanics, fluid dynamics and bioenergetics to unveil the hydrodynamic and physiological phenomena involved and their underlying mechanisms.

KEY WORDS: Locomotion, Metabolism, Fish, Energy

Introduction

Collective movement is a ubiquitous behaviour among vertebrates. It involves active, directional forward movement where animals move as a group along a common mean trajectory. Examples include cyclists in a peloton (Blocken et al., 2018), elite human runners moving in a group (Ito, 2007), migratory birds in V-formation (Portugal et al., 2014), ducklings swimming in formation (Fish, 1994, 1995), fish schools (Weihs, 1973) and long-distance movement of mammals, such as the dramatic migration of wildebeest (Williamson et al., 1988) (Fig. 1). Complex ecological and behavioural factors certainly underlie the evolution of collective locomotor behaviours, but understanding the energetic cost of movement as a group is also of considerable importance, as energy savings are proposed to be a key benefit of collective motion.

Despite the fact that energy saving is one of the most quoted functional benefits of collective movement (Weihs, 1973; Parker, 1973; Fish, 1995; Weimerskirch et al., 2001; Portugal et al., 2014; Abrahams and Colgan, 1985), we are not aware that the published

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literature contains any direct measurements that compare the total energy expenditure of a coordinated animal group versus that of a solitary individual when moving over a range of speeds. The notion of energy conservation during collective movement is often inferred from indirect indicators (such as appendage movement frequency) or based on calculations from computational fluid dynamic models (e.g. Weimerskirch et al., 2001; Usherwood et al., 2011; Portugal et al., 2014; Li et al., 2020; Kelly et al., 2023). Both approaches are indirect estimates of locomotor cost, and neither can capture both whole-animal aerobic metabolism and glycolysis, which simultaneously support the energetic cost of movement. Energy saving by collective movement has also been inferred from physiological measurements such as heart rate (Weimerskirch et al., 2001). However, heart rate is only one of four parameters of the Fick equation (see Glossary) that contributes to whole-animal oxygen (O_2) uptake (a proxy of whole-animal aerobic metabolic rate) (Farrell, 2007a,b; Haykowsky et al., 2015; Scott and Milsom, 2006), and it does not respond only to locomotor demands (Cygankiewicz and Zareba, 2013).

Some laboratory and field studies using indirect measurements have suggested that moving in a group either has no impact on energy expenditure or could actually increase energetic costs (Partridge and Pitcher, 1979; Usherwood et al., 2011). Given the lack of direct metabolic evidence for energy saving from collective motion, and mixed results from indirect metrics, there is a clear need to investigate whether and when collective group movement conserves energy using approaches that allow direct quantification of metabolic cost: aerobic, glycolytic and high-energy phosphate stores.

The objective of this Commentary is to highlight three core questions that provide the broad framework to effectively investigate the energetics of collective movement in vertebrates. (1) Why is it important to understand the locomotor performance curve and to compare group and individual performance? (2) Why is it important to measure the total energy expenditure of collective movement in comparison to energy use by individuals during solitary motion? (3) What are the challenges of studying the energetics of collective movement and what technical advancements are needed to address these questions?

To answer these three questions requires knowledge of both physiology and physics: addressing them will require a multidisciplinary approach that includes biomechanics, bioenergetics and fluid mechanics to bring collective motion and fluid dynamics together in three-dimensional (3D) analyses. Energy consumption then becomes the bridge connecting physiology and biomechanics to fluid dynamics. Because water is 50 times more viscous than air and contains 5 times less O_2 per unit volume, the benefits of optimizing locomotor costs are likely to be far greater for aquatic vertebrates than for aerial and terrestrial vertebrates. Thus, here we focus on fish as a model system to illustrate these fundamental questions related to moving as a group.

Why is it important to understand the locomotor performance curve?

Performance curves show some aspect of animal function ('performance', usually plotted on the y-axis), such as metabolic

Glossary

Cost of transport (COT)
Energy expended for moving per unit of distance travelled (sometimes also presented as mass-specific, per kg body mass). Aerobic energy expenditure only includes the energy generated by aerobic metabolism (oxidative phosphorylation). O_2 consumption is the most common measurement used to calculate COT. However, the total cost of transport (TCOT; see below) should be calculated using both aerobic and non-aerobic energy use (substrate-level phosphorylation and high-energy phosphate stores), the latter measured by quantifying EPOC (see below), and adding the non-aerobic cost to the aerobic cost (at each speed) as a function of movement speed to calculate TCOT.

Computational fluid dynamics (CFD)
Numerical simulation of fluid flow patterns to allow analysis and reconstruction of flow physics.

Excess post-exercise oxygen consumption (EPOC)
The non-aerobic cost induced by high-intensity movement at the organismic level. EPOC is estimated by the total O_2 consumed during the recovery period after the prior high-intensity movement. The ideal baseline of recovery is the lowest maintenance metabolic rate, which is termed standard metabolic rate in ectotherms or basal metabolic rate in endotherms. Often, the resting metabolic rate is used as a proxy of the lowest maintenance metabolic rate for EPOC calculation to reduce the likelihood of including the spontaneous activities that inflate EPOC. Accurate measurement of EPOC can require recording post-exercise O_2 consumption for ~24 h.

Fick equation
In the whole animal, five Fick equations describe steady-state O_2 transport at each step in the O_2 cascade system: ventilation, diffusion at respiratory organs, perfusion, tissue diffusion and cellular respiration. For example, O_2 uptake by a vertebrate from the surrounding environment can be related to internal O_2 transportation by O_2 uptake=$f_H \cdot S_v \times (Ca_{O_2} - Cv_{O_2})$, where f_H is heart rate, S_v is stroke volume, Ca_{O_2} is arterial O_2 content and Cv_{O_2} is venous O_2 content.

Fluid dynamic drag
When objects move relative to a surrounding fluid, fluid dynamic drag is the force acting opposite to the direction of motion and is caused by surface friction of the fluid on the body and by pressure changes around a moving body.

Kinetic energy
The form of energy possessed by an object due to movement. The basic equation for the calculation of kinetic energy is $\frac{1}{2}mv^2$, where m is the mass of an object and v is the velocity of the object relative to a reference.

Particle image velocimetry
An optical methodology of visualizing fluid flow by tracking the movements of small particles within a fluid. Fluid velocity is most often calculated using cross-correlation of particle image intensity from images at one time step to the next time.

Passive stability
A mode of stability control that does not require active kinematic adjustment to maintain body position. As a result, but not necessarily by definition, passive stability costs little energy to sustain.

Reynolds number (Re)
A dimensionless number that quantifies the patterns of fluid flow by measuring the ratio of inertial forces to viscous forces within a fluid. Reynolds number can be calculated as $Re=\rho uL/\mu$, where ρ is the fluid density, u is flow speed, L is a characteristic linear dimension and μ is fluid dynamic viscosity. Or $Re=uL/\nu$, where u is flow speed, L is linear dimension and ν is fluid kinematic viscosity.

**Total cost of transport (TCOT)**
Total metabolic energy (sum of aerobic and glycolytic metabolism) expended for moving a unit of mass per unit of distance travelled. Measuring TCOT requires both measuring O_2 consumption during movement and quantifying O_2 consumption during EPOC.
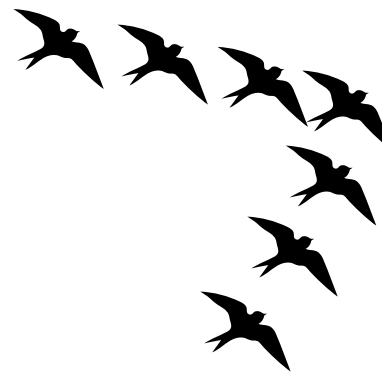
Total energy expenditure (TEE)
The total amount of metabolic energy contributed by both aerobic metabolism (oxidative phosphorylation) and glycolytic metabolism (substrate-level phosphorylation) in an animal.
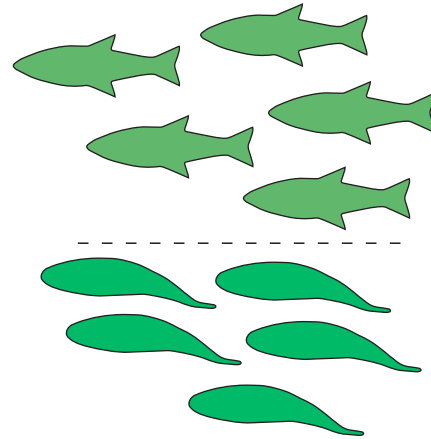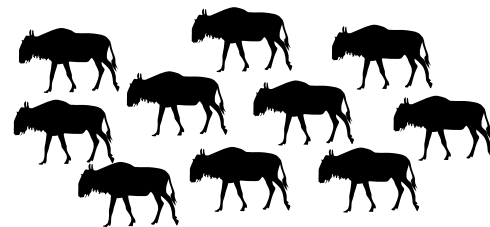

Fig. 1. Schematic representations of collective movement in fish, birds and mammals. The benefit of energetic conservation is likely to occur when animals exhibit active and directional movement in a moving fluid where drag (from either water or air) generates increased locomotor costs. (A) Indirect estimates of energy expenditure – such as tail beat frequency or heart rate – and computational models suggest that fish schools can save energy relative to individual movement. (B) The V-formation of bird flocks is proposed to save energy, which is inferred from the measurement of body kinematics or physiological parameters such as heart rate. However, birds in V-formation can also exhibit increased wing beat frequencies, indicating that direct measurement of energy expenditure is needed to compare groups with solitary birds flying at the same speed. (C) Movements of large mammal collectives, such as the wildebeest migration in Africa, could involve energy conservation when moving against the wind, but group energy savings during terrestrial locomotion have yet to be demonstrated. Animal icons from https://www.phylopic.org/.

rate, in relation to an independent variable (such as movement speed, on the *x*-axis). A wide variety of performance curves have been measured over the years (Fry, 1947; Fry and Hart, 1948;

Brett, 1964; Hoyt and Taylor, 1981; Steinhausen et al., 2008; Lee et al., 2003; Eliason et al., 2011; Claireaux and Chabot, 2016; Adams et al., 2022; Zhang et al., 2021, 2022; Zhang and Farrell, 2022), and such data are useful for characterizing animal function because they often reflect fundamental and mechanistic aspects of anatomy or physiology measured over a range of conditions. For example, metabolic energy expenditure (*y*-axis) can be compared against fluid velocity (*x*-axis) to understand how fluid dynamic drag forces (see Glossary) affect the energetic costs of locomotion. The classic work of Brett (1964) and Farrell (2007a), for example, generated numerous swimming performance curves for fish species, showing their locomotor and metabolic dynamics over a range of swimming speeds and temperatures. Schematic examples of locomotor performance curves measuring energy expenditure or power versus speed are illustrated in Fig. 2. In addition to understanding interspecific variation in the locomotor performance curve (Currier et al., 2021), a fundamental question for many biological systems is whether locomotor performance curves are linear, exponentially increasing or take the form of a concave upward curve with an energetic minimum situated higher than the lowest locomotor speeds (Fig. 2A). Understanding the shapes of performance curves provides a framework within which we can begin to hypothesize the benefits of group movement in comparison to solitary motion (Figs 2C and 3B).

Because fluid drag scales as velocity squared (Vogel, 1981), we would expect an exponential increase in movement cost as a function of speed. However, some of the published individual locomotor performance curves for fish are linear. Moreover, animals are sometimes not tested over a wide speed range (Fig. 2A). This partly reflects the challenges of testing vertebrates at both the lowest and highest locomotion speeds. An energetic study of locomotion in individual clearnose skate (*Raja eglanteria*) demonstrated a concave upward performance curve for O_2 consumption (Fig. 2A; Di Santo et al., 2017), in which swimming by individual fish at a slow speed is more energetically expensive than swimming at a somewhat faster speed. After the speed at which minimal cost is incurred, energetic costs increase exponentially following the expected relationship of drag force–fluid velocity. In addition, analyses of the power required to both fly and hover in birds and aircraft (Fig. 2B) demonstrate the concave upward power performance curve (Tucker, 1975; Alexander, 1997; Dial et al., 1997; Tobalske et al., 2003; Browning and Kram, 2005; Clark and Dudley, 2010; Warrick et al., 2012).

Why might energetic performance curves for fishes be upwardly concave? Perhaps both passive stability (see Glossary; which is lower at low movement speeds) and the need to actively generate stabilizing forces with fins and body motion contribute to increased costs at slower swimming speeds. For example, in order to generate lift during slow swimming, skates tilt their bodies at a positive angle of attack to oncoming flow (Di Santo et al., 2017), which generates lift forces that enable them to counteract the effect of gravity on their negatively buoyant bodies. When the oncoming flow is very slow, a higher body angle of attack is needed to generate lift (He and Wardle, 1986); this requires increased force generation by fin and body musculature to maintain position. Thus, animals moving at their slowest speed can incur a higher cost of locomotion than when they move at a slightly faster speed.

Knowledge of the shape and relative position of locomotor performance curves is important when collective motion is compared with the locomotion of solitary individuals (hypothesized curves shown in Fig. 2C). This is a comparison for which there are no published data yet available other than preliminary results from giant
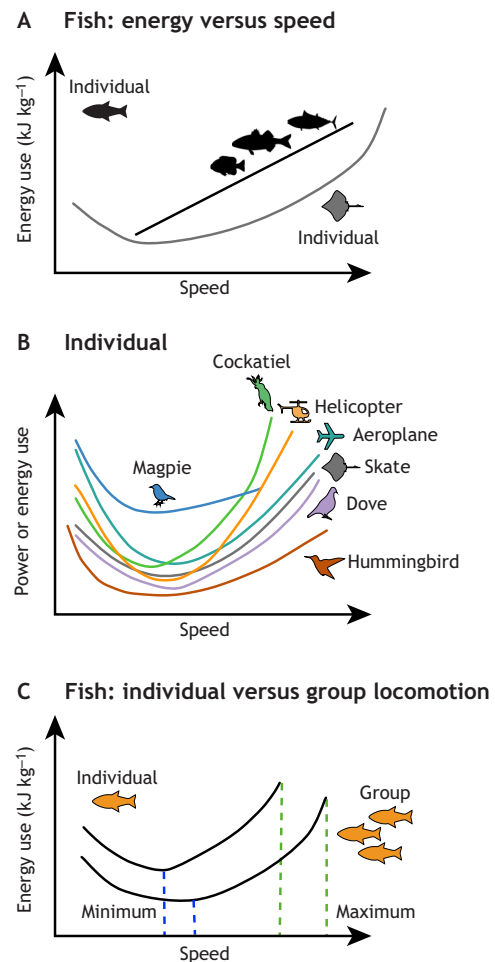
Fig. 2. Locomotor performance curves in biological and engineered systems. (A) Most published data for fish document a linear (or exponentially increasing) energy–swimming speed relationship (black line), but data for skates over a wide speed range demonstrate an upwardly concave-shaped metabolism–speed curve (grey curve), where slow movement increases whole-animal metabolic rate over movement at an intermediate speed. (B) Data for birds (measured indirectly using pectoralis muscle power) illustrate an upwardly concave performance curve as demonstrated in cockatiels, magpies (Dial et al., 1997), doves (Tobalske et al., 2003) and hummingbirds (Clark and Dudley, 2010). Helicopters (Pritchard and Kunz, 2006) and fixed-wing aircraft (l'Anson, 1969) also have an upwardly concave power–speed curve, where moving at a very low speed requires more power. The skate also has an upwardly concave locomotion energy–speed curve (Di Santo et al., 2017). It is currently unclear whether the other aquatic vertebrates have upwardly concave locomotor performance curves. The scales of speed and power differ among vertebrates and vehicles. (C) Possible locomotor performance curves for collective motion compared with locomotion of solitary individuals. At present, no available data quantify the total energetic expenditure (aerobic plus non-aerobic costs) of collective motion over a range of speeds compared with that of individuals moving alone. Also unknown is whether the performance curve for many species moving in a group is exponentially increasing or upwardly concave. Collective movement could reduce the minimum total energy expenditure of locomotion (Min) and shift the locomotor performance curve down, and/or allow increased maximal movement speeds (Max) compared with those of individuals. Animal icons from https://www.phylopic.org/.

danio comparing group versus individual energetic locomotor costs (Zhang and Lauder, 2023 preprint). That study demonstrated a concave upward performance curve with higher costs at the lowest
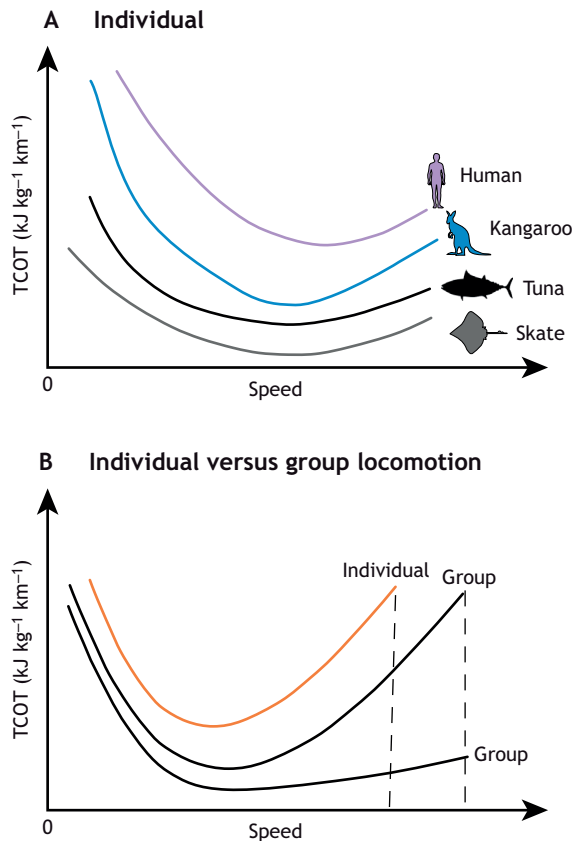
Fig. 3. Upwardly concave curve of the total cost of transport–speed curves for solitary organisms and collective groups. The total cost of transport (TCOT; see Glossary) is the total energy expenditure of moving a unit of distance. The total energy expenditure encapsulates the aerobic costs during locomotion and the additional non-aerobic costs (excess post-exercise oxygen consumption, EPOC; see Glossary) that are mostly repaid after locomotion. Most current literature measures only aerobic costs during locomotion to estimate the aerobic energy expenditure and calculate the cost of transport (COT; see Glossary). We hypothesize an upwardly concave TCOT–speed curve for vertebrate taxa when moving both individually and as a group. (A) Hypothesized schematic TCOT curves derived from experimental and modelling data for four representative species: kangaroo during pentapedal locomotion and hopping, including wind resistance (Baudinette et al., 1992); human walking (Browning and Kram, 2005; Kwak and Chang, 2023); teleost fish (tuna; theoretical expectation); and elasmobranch (skate; Di Santo et al., 2017). (B) The TCOT (including aerobic and non-aerobic energy sources) is for collective motion over a range of speeds compared with separate measurements of individuals moving alone (Zhang and Lauder, 2023 preprint). Collective movement could reduce the energetic cost over the speed range compared with the cost of solitary motion. Collective movement could also flatten the TCOT performance curve at higher speeds, which would indicate that fluid dynamic effects are particularly effective at reducing costs as vertebrates move faster. Animal icons from https://www.phylopic.org/.

speeds. Does moving in a group shift the performance curve down so that movement at all speeds is less expensive? Does collective motion alter the location of the minimum energetic cost, and/or does group motion alter the maximal sustainable speed (Fig. 2C)? Answering these questions is critical to understanding how group dynamics alter the cost of locomotion (Fig. 1).

Why is it important to measure the total energy expenditure (TEE) of collective motion?

Vertebrates use both aerobic and non-aerobic (high-energy phosphate stores and substrate-level phosphorylation) energy sources to power locomotion. Sustained locomotion at low workloads (e.g. low speeds) is predominately supported by aerobic metabolism. Although aerobic and non-aerobic metabolism have been extensively studied in terms of cellular oxidative and substrate-level phosphorylation (mostly in post-fatigue and exhausted animals; Gaesser and Brooks, 1984; Wood, 1991; Richards et al., 2002; Holder et al., 2022), most current studies on the locomotion of individual animals usually consider whole-organism aerobic metabolic rate obtained by measuring O_2 uptake ($\dot{M}_{O_2}$) during movement. Lactate levels in the blood may be measured also to confirm that energy use is at least mostly aerobic (e.g. Taylor and Heglund, 1982). Typically, the aerobic energy expenditure is measured and then the cost of transport (COT; see Glossary) is calculated. Hence, locomotor gaits at lower speeds (e.g. human walking, horse walking and trotting) have an optimal speed, showing a concave upward curve for O_2 costs to move a unit of distance. However, the O_2 costs during locomotion may show a slight decline or maintain a plateau in human running, horse galloping and kangaroo hopping (Hoyt and Taylor, 1981; Dawson and Taylor, 1973). If O_2 use alone during movement is a proxy for the energetic cost of locomotion, it is difficult to understand how humans and horses can move faster [and thus require more energy, based on the necessary increase in kinetic energy (see Glossary) and the increased drag associated with wind resistance] without actually consuming more energy. Although elastic energy cycling in tendons and other connective tissues (Baudinette et al., 1992) and the energy conversion between kinetic energy and gravitational potential energy (Cavagna et al., 1977; Margaria, 1968) can at least partially uncouple O_2 consumption from speed at low to moderate movement velocities, we suggest that the energetics of motion can be better understood by measuring both aerobic and non-aerobic costs over a wide speed range, including at high speeds.

The O_2 cost of locomotion (measured as $\dot{M}_{O_2}$) is only proportional to the aerobic ATP turnover rate under a steady state (Brett, 1962; Zhang and Gilbert, 2017). As workload increases, or at high speeds, $\dot{M}_{O_2}$ gradually decouples from the ATP turnover rate (Milligan, 1996; Farrell and Clutterham, 2003), as a higher proportion of short-term ATP production is supported by high-energy phosphates and substrate-level phosphorylation of pyruvate to ATP without O_2 consumption (Hochachka and Mommsen, 1983). The glycolytic pyruvate supply results in a substantial ATP supply from substrate-level phosphorylation, which produces lactate. Fast-twitch 'white' muscle fibres are mostly fuelled by glycolysis to support the additional thrust needed at higher movement speeds (Jayne and Lauder, 1996; Moyes et al., 1992). Glycolytic contributions to locomotion have been measured in studies using blood lactate (Taylor and Heglund, 1982) and lactate kinetics (isotope-labelled lactate to distinguish lactate appearance and disposal) (Omlin and Weber, 2010; Teulier et al., 2013; Weber et al., 2016). The confounding factors of using blood lactate accumulation to estimate the glycolytic costs of locomotion are that (1) blood lactate accumulation is a net result of lactate appearance and disposal (Weber et al., 2016), (2) specific organs, such as fish hearts, also oxidize lactate (Gemelli et al., 1980; Milligan and Farrell, 1991), and (3) lactate can become fuel for oxidative phosphorylation in slow-twitch 'red' muscles (Brooks, 2018). This enables sustained muscle performance relying on both oxidative and substrate-level phosphorylation (Conley et al., 2001), and is critical to allow human cyclists, for example, to maintain 80% of maximum power output for approximately 30 min (Hoppeler et al., 1985).

Despite important interactions between oxidative and substrate-level phosphorylation in vertebrate physiology, few studies measure both the aerobic and non-aerobic cost of locomotion in individuals over a wide speed range (e.g. Lee et al., 2003; Svendsen et al., 2010). No published study, to the best of our knowledge, has measured both the aerobic and non-aerobic costs for active, directional swimming during collective motion and compared these costs with those of solitary individuals moving at the same speed. Consequently, a substantial proportion of the energetic contribution from high-energy phosphate stores and glycolysis may be overlooked (Wood, 1991; Scarabello et al., 1991, 1992; Richards et al., 2002), at least in studies of fish locomotor dynamics; yet, for faster speeds, this contribution can be substantial (~50%; Lee et al., 2003; Zhang and Lauder, 2023 preprint). Vertebrates repay the O_2 deficit incurred at locomotor speeds above the aerobic threshold through a prolonged and elevated aerobic metabolic state during the post-locomotion recovery time. The total O_2 cost for recovery is measured as excess post-exercise O_2 consumption (EPOC; see Glossary; Brett, 1964; Gaesser and Brooks, 1984; Brooks, 2018). Hence, the total energy used during locomotion must be determined by measuring $\dot{M}_{O_2}$ (the aerobic contribution) and by quantifying EPOC. By modelling how the non-aerobic contribution changes with speed (Lee et al., 2003), the aerobic and non-aerobic (EPOC) contributions can be integrated to estimate the total energy expenditure (TEE; see Glossary) at each speed and over a speed range. Knowing the TEE and movement speed allows calculation of the total cost of transport (TCOT, aerobic plus non-aerobic energy in kJ per kg per km; see Glossary), which generates the performance curve of the total energy used per distance travelled. Based on the published studies and principles of physics (kinetic energy and fluid drag as functions of speed), we hypothesize that TCOT curves of vertebrates across a diversity of locomotor gaits and a wide range of speeds can show a concave upward shape (Fig. 3A).

What is the effect of collective movement on TCOT curves? To our knowledge, there are currently no published data available to answer this question other than some preliminary results (Zhang and Lauder, 2023 preprint). Here, we present several possible effects of collective movement on the TCOT; these suggestions can serve as hypotheses for future experimental analyses (Fig. 3B). If we assume that group movement reduces energetic costs, the TCOT curve for an animal moving in a group could be shifted downward with reduced costs across all speeds compared with the curve for solitary individuals. Another (not mutually exclusive) possibility is that group motion involves hydrodynamic interactions that increase in benefit as movement speed increases, resulting in a flattening of the TCOT curve and only a slight rise in TCOT as speed increases (Fig. 3B). Testing these hypotheses will require experimental measurements of whole-animal metabolic aerobic and non-aerobic energy use in collectively moving vertebrates.

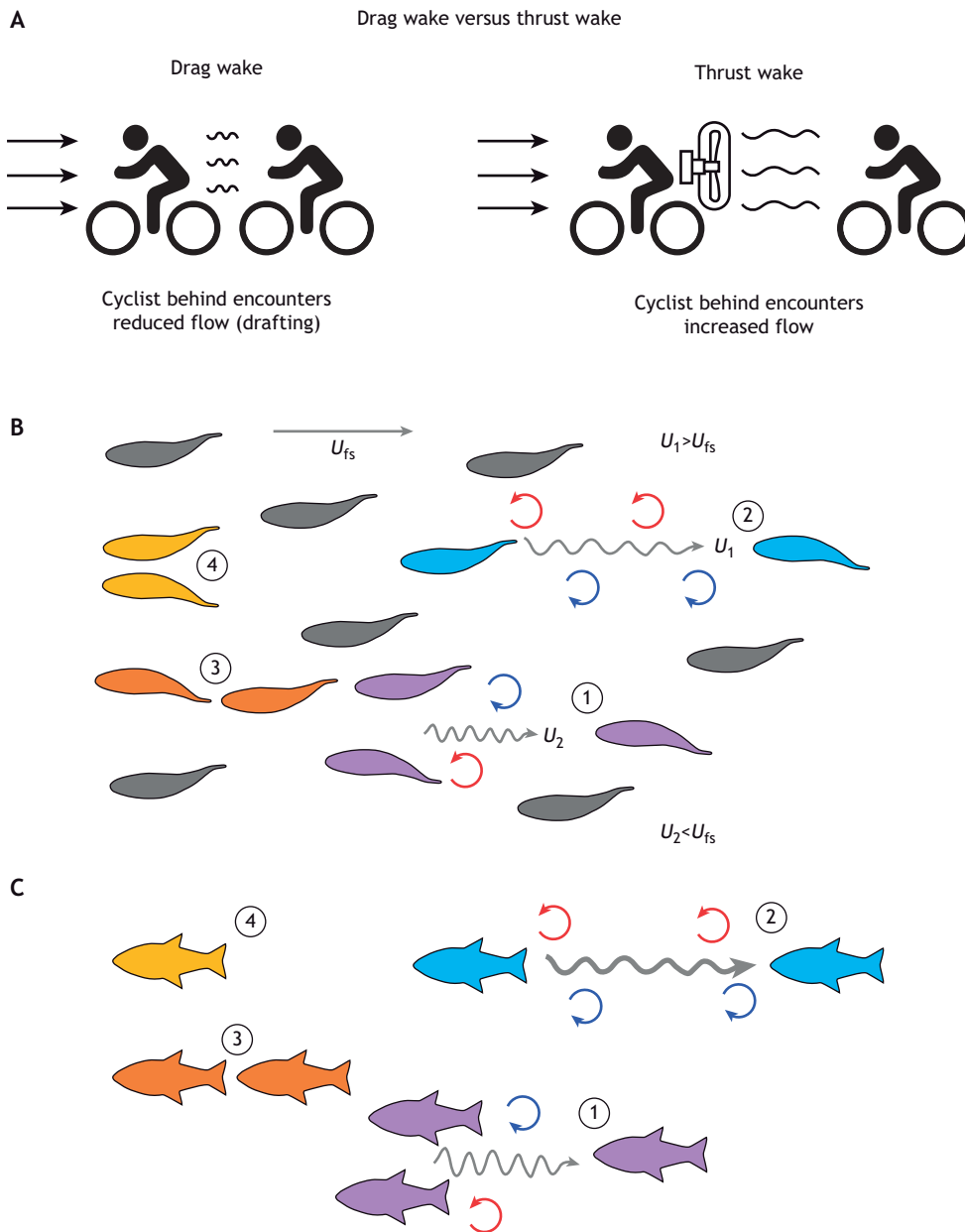### What are the challenges of studying the energetics of collective movement?
Investigations of the energetics of collective movement are complicated by the difficulty inherent in directly measuring metabolic energy expenditure in animals moving freely in nature as a collective. For example, considering birds moving across the airscape in a V-formation (Fig. 1B), how should one measure both aerobic and glycolytic metabolism of these animals over a range of speeds, and also gather data for solitary birds flying at the same speed and under the same aerodynamic conditions? This is clearly a challenging proposition. Indirect measurements of energy expenditure such as wing beat frequency provide ambiguous

results, with at least one study demonstrating increased wing beat frequency when birds are in a V-formation, suggesting increased locomotor costs rather than the expected energy savings (Usherwood et al., 2011). For swimming fishes and other aquatic organisms, computational models demonstrate a variety of mechanisms by which collective movement could save energy (Fig. 4B,C). However, such mechanisms need to be validated using direct experimental measurements, and models are usually speed specific and not often suitable for generating performance curves where high-speed locomotion requires simulation at high Reynolds numbers (see Glossary).

Furthermore, in nature, animal groups are often moving at considerable speeds, which are difficult to replicate in the laboratory. Bird V-formation flying is an obvious example of vertebrates moving at a high speed as a group, and fish schools can move at speeds well beyond those typically studied in the laboratory [~5 body lengths (BL) s^{-1} for sustained and prolonged swimming; see Castro-Santos, 2005; Fig. 5]. The collective movement of fishes can reach speeds of ~20 BL s^{-1} (Brehmer et al., 2011; Misund and Aglen, 1992). During high-speed movement, drag forces are exponentially greater than at lower speeds; hence, the potential advantage of being in a group could be considerably magnified. The increased energetic workload at high speeds (>50% of the highest sustained locomotor speed) is supported by both aerobic and non-aerobic energy sources (largely glycolysis) (Brett, 1964; Lee et al., 2003; Laforgia et al., 2006). If collective movement can reduce the energetic need for glycolysis, then vertebrates moving in groups will experience shorter recovery times, and would be able to repeat high-speed locomotion more rapidly, which could be advantageous for feeding or escaping predators. We hypothesize that the benefits of this energy conservation will be greatest at higher movement speeds, resulting in a down-shift of the energetic performance curves at higher speeds (Figs 2 and 3). We suggest that prioritizing the quantification of the locomotor energetic performance curve over a wide range of speeds will inform the focus of investigation for 3D high-speed kinematics, group structures and fluid dynamics. This will help to indicate potential mechanisms by which collective movement might conserve energy.

Measuring whole-animal aerobic and glycolytic metabolism
To directly compare the TEE of an animal moving as part of a group with that of a solitary individual requires respirometry measurements made on groups and solitary individuals separately (Parker, 1973). Given the different masses of groups and individuals, different sizes of respirometers may be needed to obtain reliable signal-to-noise ratios (larger containers and smaller biomass often result in a lower signal-to-noise ratio; Zhang et al., 2019; Prinzing et al., 2021; Zhang, 2021). In addition, quantifying EPOC can require continuous measurements for up to 20 h post-exercise, and shorter measurement periods can result in underestimates of glycolytic metabolism. For example, measuring EPOC for 4–6 h in fishes can result in non-aerobic metabolism being underestimated by up to ~50% (Zhang et al., 2018). In humans, EPOC can last up to 24 h. This duration is directly related to exercise duration and intensity (Laforgia et al., 2006). Currently, automation in aquatic respirometry enables the measurement of $\dot{M}_{O_2}$ and EPOC on the same testing objects over a prolonged period (Steffensen et al., 1984; Svendsen et al., 2016; Zhang et al., 2017), paving the way to calculate TEE and TCOT for collective behaviour during aquatic locomotion. When considering the challenges of quantifying metabolism over a speed range and comparing groups with individuals, we believe that studies of fishes moving in

A

Drag wake versus thrust wake

Drag wake

Thrust wake

Cyclist behind encounters
reduced flow (drafting)

Cyclist behind encounters
increased flow

B

U_{fs}

$U_1 > U_{fs}$

U_1

U_2

$U_2 < U_{fs}$

C

Fig. 4. Hydrodynamic mechanisms that reduce locomotor costs during collective movement. (A) In the air, drafting behind another individual is known to save energy as a result of the reduced incoming flow following the leading individual, which is a drag wake (left). In contrast, leading fish generate an increased flow behind, a thrust wake. This is the equivalent of a leading cyclist with a large fan on their back accelerating flow behind, which increases the incoming flow to a trailing cyclist (right). Terrestrial animals moving collectively could save energy during locomotion by locating themselves in a drag wake directly behind other individuals. However, what can fish do? (B,C) Several fluid dynamic mechanisms of energy savings have been demonstrated that could apply to fish within a school. Bottom (B) and side (C) views of a fish school demonstrate that energy saving can occur by (1) reduced oncoming velocity U_2 from free-stream velocity U_{fs} (Weihs, 1973), (2) the Knoller–Betz effect of leading-edge suction reducing costs for a trailing fish even in the face of increased flow U_1 (Jones et al., 1998; Saadat et al., 2021), (3) added mass 'push' from follower to leader reducing costs for the leader (Fish and Hui, 1991; Kurt and Moored, 2018; Saadat et al., 2021) and (4) wall effects from neighbouring fish, where swimming next to another fish reduces swimming costs (Daghooghi and Borazjani, 2015; Li et al., 2020). Counter-clockwise (red) and clockwise (blue) arrows indicate the direction of fluid vorticity at that location.

laboratory respirometers promise to provide the best first estimates of the energetics of collective behaviour (Zhang and Lauder, 2023 preprint). Similar analyses of bird flight and terrestrial mammal locomotion pose experimental challenges that may only be resolved using new technologies.

Measuring 3D kinematics and group structure

In order to understand why collective movement energetics might differ from those of solitary individuals, we need to know how animals are moving with respect to each other in three dimensions (Major and Dill, 1978; Herbert-Read, 2016). Moving near other animals in a group introduces a panoply of fluid dynamic mechanisms that could be involved in energy saving (see Fig. 4, for example). We need to know: (1) the 3D distances among individuals, (2) whether inter-individual distances change with speed, and (3) how the body and appendage motion of animals in a group differs from that of solitary individuals. Yet, many challenges are involved in obtaining such data.

Tracking the kinematics of individuals in 3D space is necessary for a complete picture of collective movement dynamics: animals interact with the pressure and flow fields generated by other individuals in three dimensions (Dabiri et al., 2014). However, tracking individual kinematics and group structures is commonly conducted in two dimensions. Two-dimensional (2D) studies have been instrumental in revealing simple motions of individuals within a school that suggest energetic savings from collective movement (Li et al., 2020; Thandiackal and Lauder, 2023). Even with the advent of effective and open-source tracking software (Walter and Couzin, 2021; Lauer et al., 2022; Chiara and Kim, 2023; Pereira et al., 2022), 2D analyses continue to dominate studies of animal kinematics. Some recent studies document 3D V-shape formation for bird flocks (e.g. bald ibises, *Geronticus eremita*; Portugal et al., 2014) and pairings within the flocks (e.g. jackdaws, *Corvus monedula*; Ling et al., 2019). There are, of course, many difficulties in obtaining multi-camera calibrated 3D data on multiple individuals to reconstruct their body and appendage motion (not
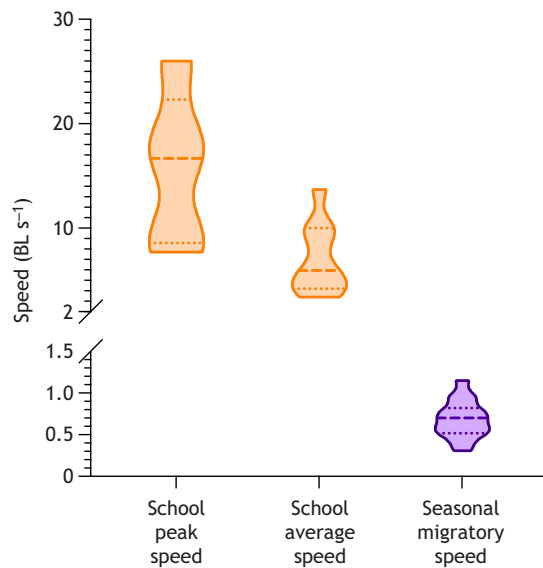
Fig. 5. Swimming speeds of fish schools and seasonal migratory speeds in the field. The truncated violin plots (outline, frequency distribution; dashed line, median; dotted lines, 25–75 percentile) are based on a summary of swimming speed data from the literature (see Table S1 for details). We report the relative swimming speed (in body lengths per second, BL s^{-1}) to account for the size range of species studied. Fish schools swim over a wide range of swimming speeds in natural habitats, and schools can swim at high speeds (>6 BL s^{-1}) when moving in open-water habitats. Schools can reach a peak speed of almost 16 BL s^{-1}, which is nearly 2.5 times the average speed. Seasonal migratory speeds of around 1 BL s^{-1} are most commonly obtained from animal-borne sensors or data loggers, and data in the current literature skew toward large migratory species as a result of the technical limitations of attaching relatively large tags to small individuals.

just body locations), including the computational challenges in segmenting overlapping individuals that are undergoing constant and dynamic changes in relative position. However, we believe that such 3D kinematic data will be critical to understanding the mechanistic bases of any observed differences in metabolic data between groups and solitary individuals, and for assigning one or more of the known fluid dynamic mechanisms to subgroups within the collective (Fig. 4).

3D tracking of both solitary individuals and those in a group is ideally done simultaneously with metabolic measurements to validate that changes in metabolic rate are associated with specific body kinematics or 3D group formations. With simultaneous kinematic and metabolic data, we can better understand the energetic performance of the animals in the group.

Quantifying 3D fluid dynamics within groups
In addition to understanding the metabolism and kinematics of collective motion, ideally we would also like to understand the fluid dynamic environment that animals are moving in. Particle image velocimetry (PIV; see Glossary) has provided a wealth of information on animals moving through the water (Drucker and Lauder, 1999; Nauen and Lauder, 2002) and air (Johansson and Hedenström, 2009; Hedenström et al., 2010; Lentink et al., 2007), and the extension of 2D analyses to 3D is becoming increasingly common (Flammang et al., 2011; Mendelson and Techet, 2015; Elsinga et al., 2006). PIV provides valuable experimental insight into the kinematic interactions of individuals with patterns of fluid motion; it enables measurement of drag and thrust wakes and shows

where individuals are located within these flow regimes (Fig. 1A, Fig. 4). Velocity vector fields are the primary data provided by PIV, from which the surface pressures or locomotor forces can be estimated for freely moving animals (Peng et al., 2007; Dabiri et al., 2014; Thandiackal and Lauder, 2020; Calicchia et al., 2023).

There are many challenges to understanding 3D fluid dynamics within fish schools, not least of which are the issues of resolution: relevant flow structures can be small, shadows caused by individuals within the group can block laser illumination, and the rapidly changing positions of individuals necessitate high image-capture rates to resolve flow dynamics. Computational fluid dynamic (CFD) analyses (see Glossary) that employ a variety of approaches to better understand group collective dynamics (Dong et al., 2006; Mittal et al., 2008; Borazjani et al., 2012; Fish et al., 2016; Zhang et al., 2023) can address these challenges to some extent, and such analyses are an important complement to experimental measurements. CFD allows a detailed understanding of the flow physics within collectives, does not suffer from resolution issues, and can generate detailed flow patterns within groups that are not subject to experimental limitations and the challenges of working with live animals.

The typical range of Reynolds numbers used for CFD simulation of collective fish movement is 1×10^3–1×10^4. However, even small fish swimming near or at their maximum sustained swimming speed can easily reach a Reynolds number one or more magnitudes higher, and large animals will move at even higher Reynolds numbers. This poses a challenge for computational approaches.

Conclusions and prospects
Given the considerable current interest in the collective dynamics of animal motion and the common view that moving in a group saves energy relative to moving as a solitary individual, it is surprising that there are so few experimental data that document the energetic advantage of group motion. In order to understand whether and how collective motion influences the energetics of movement, it is necessary to directly measure both whole-animal aerobic metabolism and glycolysis, which together provide the energy (ATP) that powers locomotion. Then we can demonstrate how group characteristics – such as the spatiotemporal positioning of individuals – can take advantage of fluid dynamics that may enable energy conservation. We advocate here for the direct measurement of energetic performance curves for collective movement and then a direct comparison with similar data for solitary individuals moving at the same speed and in the same experimental fluid conditions. Such analyses promise a comprehensive picture of the energetics of collective movement when coupled with experimental data on the kinematics and fluid dynamics of the group.

Finally, we note that one of the key components of predicting global animal distributions and abundance is an understanding of environmental factors that affect the ability of animals to move. Locomotor performance curves can serve as the foundation on which to build ecological models. Other environmental factors, such as acidity, temperature and O_2 availability, can shift and shape these performance curves, and understanding how these factors shape collective behaviour is a key challenge for the future.

Competing interests
The authors declare no competing or financial interests.

Data availability
This article has an associated ECR Spotlight interview with Yangfan Zhang.

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