Energetics of Swimming and Flying in Formation

Formation movement during swimming and flying has been hypothesized to reduce an individual animal's energy expenditure. Individuals in a formation distort the flow pattern, creating vorticity in their wake. Vorticity is produced from lifting surfaces and organized as wing tip vortices, from oscillating hydrofoils in the form of a thrust-type vortex street, and by flow separation from rigid bodies arranged as a Kármán vortex street. The relative velocity induced by vorticity shed from leading animals can be used to lower the drag and energy expenditure on trailing individuals when ideally positioned in the vortex wake. The wing tip vortices generated by birds reduce induced power as determined by wing tip spacing when flying in V-formation. The optimal configuration to maximize energy savings in fish schools is a diamond shape. Vorticity shed from rigid bodies, such as cars, cyclists, or ducks, produces a region of low relative velocity immediately behind the leader fostering drag reduction and increased energy savings by traveling in a single-file formation.

Key Words: *formation locomotion, schooling, drag, vorticity, drafting*

Numerous species of animals move in polarized aggregates or defined formations. It has been suggested that these social behaviors evolved for protection against predation, locating food resources, mating efficiency, pooling orientation information, greater tolerance to toxic substances, and energy economy.[1–4] Formation movement as a mechanism for energetic reduction of locomotor effort is generally accepted for automotive and cycling competitions, which use an advantageous technique of "drafting" or "slipstreaming."[5–7] Because animals move in highly organized formations, such as V-formations of flying geese and schools of fish, the idea that these spatial patterns reduce energy expenditure has been enticing, particularly for migrations, where locomotor costs are the

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predominant component of the animal's energy budget. The effective use of energy provides an important advantage in short term survival and evolutionary success.[8]

The opinion that animals move in highly organized formations to reduce locomotor energy costs has been irresistible, but direct evidence has been elusive. The three-dimensional complexity, uncontrolled and inconsistent positioning of individuals in the formation, and large size of individuals and the collective formation deterred experimentation to test the hypothesis of energy conservation! [9] [10] Previous analyses have focused on aero- and hydrodynamic models.[3,11–16] These models predicted significant energy savings when animals were moving in the appropriate formations with an exact spacing between individuals. However, the optimal configuration was seldom realized.[8,13,16,17] Despite these limitations, empirical studies have demonstrated that formation movement can reduce energy cost in accordance with prediction.[8,10,18,19]

This article reviews the available information concerning formation movement with regard to energy conservation. Although the primary focus is on swimming and flying, the common theme is how flow, of water or air, affects formation movement energetics. Correspondingly, terrestrial formations which realize energy savings from fluid flow also will be discussed.

VORTICITY ASSOCIATED WITH FORMATION MOVEMENT

The physical basis for energy savings from formation swimming and flying relates to the interaction of the body or propulsive appendage (e.g., wing, fin) with the fluid medium. As a body or appendage moves through a fluid, it distorts the velocity field around itself and in its wake. The distortion is represented by circulating masses of fluid with irrotational flow called vortices. Three distinct vortex systems (Figure 1) allow energy savings by animals moving in formation:

1. Tip vortices from foils generating lift.[20] Tip vorticity is produced as a consequence of the pressure difference over a three-dimensional foil generating lift. **A** foil directed into a flow with a positive angle of attack will have a faster flow on its upper surface than along the lower surface. Relative to the flow, the difference in velocity around the foil develops a

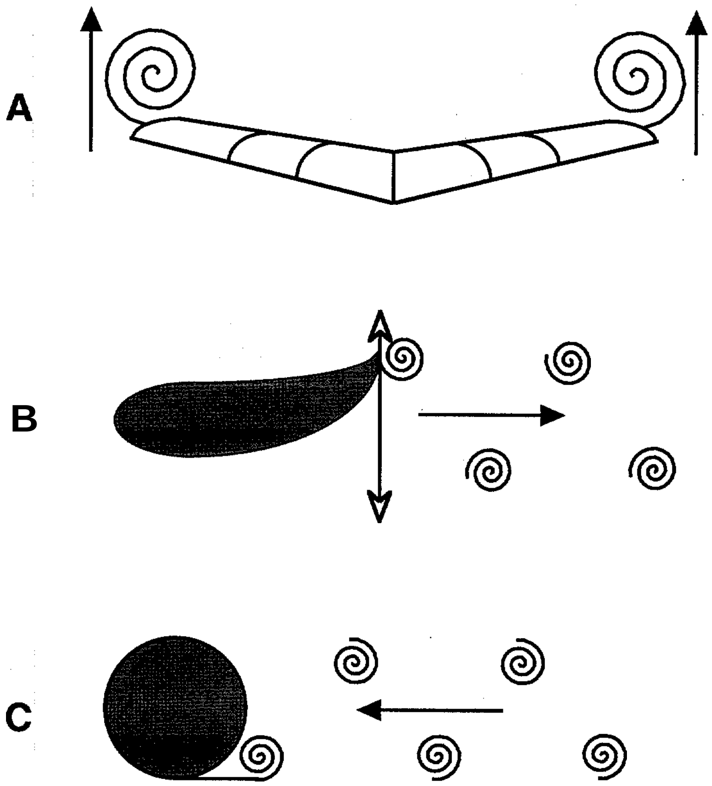

FIGURE 1 Vortex patterns used by trailing organisms for energy savings. Vortices in A are shed from the tips of a lifting surface such as the wings of birds, the vortex street in B is a thrust-type generated in the wake of an actively swimming fish, and in C the Kármán vortex street is produced in the wake of a bluff body. Solid arrows indicate the direction of the induced velocity; open arrows indicate the direction of oscillation of the fish tail.

theoretical "bound vortex" which creates circulation. The intensity of the circulation is dependent on the difference in velocities. The circulation integrated over the entire span of the foil is directly proportional to the total lift. According to the Bernoulli theorem, the side of the foil with the faster flow will have a lower pressure compared to the side with the slower flow. The pressure differential generates a force, lift, that is normal to the flow.

Because foils such as wings are finite in span, the pressure differential between the wing surfaces induces a flow around the wing tips. Fluid leaks from high pressure side of the wing to the low pressure side in the spanwise direction creating a vortex at the wing tip (Figure 1A). This vortex encounters the main flow over the wing and becomes sheared. As the tip vortex is shed from the wing, it leaves as a vortex trail. The tip vortex is positioned slightly inboard of the wing tip. The bound vortex in combination with the pair of oppositely circulating tip vortices generated from each end of the wing form a "horseshoe vortex" (Figure 2).

The generation of tip vortices is associated with energy loss from the wing into its wake. Tip vortices add to the total drag on the wing as the induced drag component. Induced drag is the drag incurred from the production of lift as fluid is deflected around a finite wing.[20] Despite the energetic disadvantage of the obligate generation of tip vortices, it has been hypothesized that birds flying in formation may augment lift and reduce induced drag.[13]

2. Thrust-type vortex street generated by an oscillating foil.[21] In generating thrust, an oscillating foil will produce a series of counter-rotating vortices in its wake (Figure 1B). The vorticity in thrust production is necessary to transport momentum from the foil into the fluid. Each vortex is formed as the reversal in direction of the foil requires a reversal in circulation of the bound vortex. At the end of each half-stroke, the bound vortex is shed from the foil and as the foil is reaccelerated in the opposite direction a new bound vortex is formed with a reversed circulation.[20] The shed vortex is known as the "stopping vortex." The oscillating motion of the foil thus produces two parallel trails of staggered vortices perpendicular to the plane of oscillation and with opposite circulations. The direction of the circulation is oriented so that the tangential velocity is parallel to the trails and directed posteriorly between the trails and anteriorly on the outside of the trails.

The thrust-type vortex street is a two-dimensional representation of the flow field shed from an oscillating foil. In three dimensions the stopping vortices are actually connected by tip vortices, forming a folded chain of vortex rings.[20] Such a flow field is essential to the generation of thrust in swimming fish. Although the vorticity convected into the wake represents an energy loss, the vortex street has possibilities for reduction in energy costs by schooling fish.[3,22]

3. Vortex street shed from a rigid body.[20] As a bluff (non-streamlined) body moves through a fluid, the flow about the body is non-steady. Flow

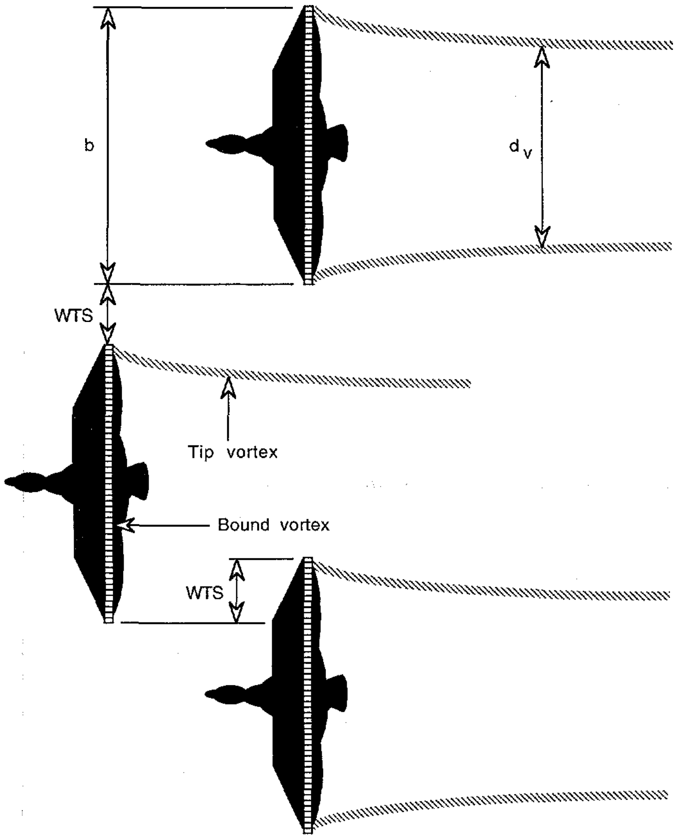

FIGURE 2 Diagrammatic representation of the horseshoe vortex system generated by gliding birds. The bound vortex encircles the wings and is connected to the tip vortices shed behind the bird. WTS is the wing tip spacing shown for overlapping and non-overlapping wings. The wing span, *b*, and the horizontal distance between wing tip vortex centers, d_v, are shown. The left vortex tip of the leading bird was removed for clarity.

separates alternately from each side of the body producing two staggered rows of vortices which are shed into the wake. Like the thrust-type vortex street, all the vortices in one row rotate in the same direction, but opposite to that of the other row (Figure 1C). However the rotation of the vortices is opposite to the pattern found in the thrust-type vortex street. This flow pattern around a bluff body is known as the Kármán vortex street. The vortex pattern is stable for a long distance downstream if the distance between successive vortices on the same side are 3.56 times the distance between the two rows.[20]

The vortex pattern occurs at a Reynolds number, R_L, range of 40–10,000.[7,20] Reynolds number is a dimensionless ratio of the inertial to viscous forces and is calculated as:

$$R_L = UL/v \tag{1}$$

where U is the flow velocity, L is a characteristic length of the body, and v is the kinematic viscosity of the fluid (i.e., ratio of density to viscosity). The frequency of vortex shedding, f_v, is dependent on the Strouhal Number,[23] St, where:

$$f_v = U\mathrm{St}/d \tag{2}$$

and d is the characteristic diameter of the body. St is dependent on the Reynolds number, R_d, when using the diameter (d) or maximum width of the body as the characteristic length. Between R_d of 10^3 and 10^5, St is constant at 0.2. Below R_d 10^3, St decreases and below R_d of 40 no vortices are shed; whereas above $R_d = 3 \times 10^5$, St increases exponentially with a vortex street persisting up to ten.[20,23]

The generation of the Kármán vortex street has been suggested to reduce the cost of locomotion in bodies that move in single-file formations between the parallel vortex rows. Race cars, cyclists, and swimming ducklings are arranged in such formations and can provide an appropriate test situation for determining energy economy.[6,7,19]

RELATIVE VELOCITY AND POSITION

The benefit of being situated in the vortex wake of another body relies on the relative position of the bodies. The vorticity shed from the leading body influences the drag and/or lift on the trailing body by affecting its relative velocity. The relative velocity is calculated as the vector sum of the longitudinal velocity over the body and the tangential velocity of the vortex. The tangential velocity (U_r) is directly related to the circulation (Γ) of the vortex and inversely related to the circumference according to:

$$U_r = \Gamma/2\pi r \tag{3}$$

where Y is radius of the vortex.[20] With similar circulations, smaller vortices will have higher velocities. Furthermore, the closer an object is to the vortex core the higher the velocity it will experience and the greater momentum it can extract from the moving fluid.

If the body is moving at a given velocity and oriented parallel to the tangential velocity, the body will experience a reduction in the relative velocity. Because the drag is directly proportional to the velocity squared, a decrease in the relative velocity can decrease drag and the associated energy expenditure.

Optimal positioning in a formation for maximum reduction in locomotor effort is dependent on the mechanism of vortex generation. The three vortex systems described above show either differing rotations of the vortices or differing orientations of the vortices with respect to their spacial plane.

Tip vortices are predicted to reduce the induced drag on birds or airplanes flying at the same altitude in line abreast, echelon, or V-formations.[13,24] All three formations provide average induced drag reductions of 14%.[24] The advantage of the V-formation is that it avoids collisions between wings of adjacent birds as could occur in line abreast formation. Only the V-formation permits a more equitable distribution of drag reduction between individuals; however, the center bird experiences almost the same drag as when flying alone.[11,24] Trailing birds experience a stronger upwash from a more fully developed vortex flow, although the effect will be dominant on only one side of the bird.

The V-formation would tend to be self-stabilizing due to the variation in the relative velocity along the breath of the formation. Individuals flying ahead of the other members of the formation will experience a higher relative velocity requiring greater input of power to maintain speed. By maintaining the same power as others in the formation, the individual would naturally fall back into position." For the leader which encounters the greatest resistance, its behavior is unclear and described as altruistic. Frequent oscillations, break-ups, and reformations along the length a V-formation particularly in windy conditions indicate potential high energy requirements when leading.[25,26] Leaders may experience some energy savings if the formation of the V is swept.[25] In the swept V, the depth from leader to neighbors is less than the depth between the other birds."[14] The middle of the formation has more of a line abreast arrangement and provides energetic advantages for the leader.

The thrust-type vortex system reduces the drag on individuals positioned parallel and lateral to the street. For schooling fish which can use this type of vortex system, a low relative velocity and high energetic advantage is achieved by a fish swimming diagonally behind another. Due to the rotation of the vortices, a fish following directly behind another will experience a higher relative velocity and would have to expend a greater amount of energy.[3]

Conversely, the rotation of vortices in a Kármán vortex street or drag-type vortex system is the reverse to that generated by lateral oscillations of fish. The flow regime in the wake of the Kármán vortex street produces a low relative velocity directly behind the leading body. In this case, bodies following in a single-file formation will experience reduced drag and energy cost.

THEORETICAL MODELS AND EMPIRICAL RESULTS

The use of models, both mathematical and conceptual, has been the traditional approach in understanding the energetic advantage of formation travel. It has been recognized that these models are based on simple engineering concepts and predict optimal or perfect solutions.[25] Although solutions to the models may be overly optimistic, a model provides the framework for constructing a hypothesis which can then be tested by collecting actual performance data on the animals. In situations where energy economy is of prime importance for survival, selection would be strong for mechanisms that increase energy conservation.

Based on the different vortex systems presented above, three examples of formation travel where energy conservation is necessitated are examined.

Birds in V-formation

Analyses of formation movement by flocks of birds have used aerodynamic models for fixed wing aircraft. The rationale for omitting the effects due to the flapping action of the wings is that the drag due to flapping is of low magnitude provided that the ratio of tip flapping speed to flight speed is low.[11,12] The major energy losses are due to the profile (resistance due to skin friction with flow) and induced drags, which are identical to losses assuming a fixed wing. Kestrels (*Falco tinnunculus*) exhibit continuous spanwise vorticity during fast flight, although the flapping motion of the wings does produce some vertical and horizontal changes in the trailing vortices.[27]

The vortices generated by the wing produce a downwash inboard of the wing tip which is related to the lift distribution of the wing and an upwash outboard of the wing (Figure 2).[11] This upwash from the tip vortex effectively acts as a upcurrent so that less induced power is required to maintain lift for a trailing bird. The induced drag is reduced, but profile drag remains unchanged.

The potential savings to birds flying in formation in the same horizontal plane is dependent on the wing-tip spacing. Wing-tip spacing, WTS, is defined as the distance between two bird bodies minus the mean maximum wingspan (Figure 2).[16] A decrease in WTS by a trailing bird will position its wing in the upwash of trailing vortex of the leader. The power needed for generating lift by the trailing bird is reduced. However with further decrease in WTS and thus greater overlap of the wings, the trailing bird is negatively impacted as its wing experiences the downwash from the leader. In between, there is an optimal position for WTS that maximizes energy savings.

An early model considered the line-abreast formation for birds flying formation.” The wing distribution was assumed to be elliptical, profile drag on individual birds was assumed to be constant and birds were assumed to fly in the same horizontal plane. The formation pattern was limited with positive values of WTS. Despite this constraint, a flock of 25 individuals was predicted to show a decrease in the ratio of the induced drag of the formation compared to a solo flyer. The energy savings would allow a 7 1% increase in flight range with a cruising speed 24% lower than for a single bird.

Refinement of the analysis of flying in formation employed Munk’s stagger theorem. This theorem states that any formation of lifting bodies may be staggered so that the bodies in the same horizontal plane are displaced parallel to the flightpath without changing the total induced drag on the system.[11,26] Thus the results of line-breast formations hold for other formations such as echelon and V-formations. By considering staggered formations, the effects of overlapping wings may be determined.[13 14,16,25]

The WTS that maximizes the induced power savings (WTS,,,) is predicted from the horizontal distance between vortex centers (d_v) of the horseshoe vortex of a fixed wing (Figure 2). The d_v is calculated from:

$$d_v = (\pi/4)b = 0.78b \tag{4}$$

where b is the wing span (Figure 2).[14,16] **A** more rigorous model[28] determined that d_v was actually $0.89b$. WTS_{opt} is calculated according to:

$$WTS_{opt} = b(1 - 0.89). \tag{5}$$

For example, a Canada goose *(Brunta canadensis)* with a wing span of 1.5m will have a WTS_{opt} with an overlap of 0.165 m. Maximum energy savings of 51% above a solo flyer is predicted for a formation of nine geese maintaining an exact overlap of 21.3% of the semispan (Figure 3).[13] The rapid drop in energy savings occurs as WTS increases or decreases.

When field observations were made of WTS in V-formations, considerable variation is noted.[16,25–29] WTS showed highly skewed distributions for pinked-footed geese *(Anser brachyrhynchus),* Canada geese *(Bruntu canadensis),* and white pelicans (*Pelecanus erythrorhynchos*), with the latter two species exhibiting negative median values of WTS. *Bruntu* had a median WTS of 19.8 overlap which corresponded to an energy savings of 36% compared to the energy expenditure of a solo flyer.[28] The positive WTS for *Anser* coincided with a savings in induced power of only 14%.[16] *Brantu* are more precise in their WTS than other birds, such as the brown pelican *(Pelecanus occidentalis),* in that twice as many geese maintain the optimal position within the formation compared to the pelicans.[29]

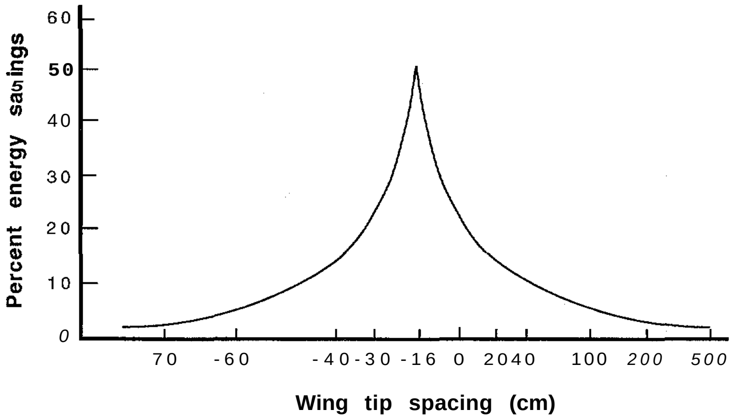

FIGURE 3 The relationship between wing tip spacing and induced power savings for V-formations of Canada geese. The curve was redrawn from Badgerow and Hainsworth[13] which was based on the model by Lissaman and Shollenberger.”

The model using the horseshoe vortex system indicates that energy savings is influenced by the combination of WTS and flock size.[11,15] Greater energy savings are achieved with large flocks and values of WTS approaching WTS_{opt}. For large values of WTS greater than 1.5 times the wing span in which energy savings are low or null, flock size has little effect.'' Despite the increased energy savings with increasing flock size, formations are not infinite. Integrating foraging theory into the aerodynamic model predicts an optimal flock size that maximizes energy efficiency (net energy gain/energy expenditure) under defined parameters of speed, distance and time of migration.[15] An individual within the optimum size flock would be *60%* more efficient than a solo flyer.

Norberg noted that the overall energy savings during formation flight would be smaller than predicted, because the induced power is only a small proportion (approximately 20%) of the total power.[30] Assuming that profile drag is unaffected, the maximum energy savings 71% estimated by Lissaman and Shollenberger'' is reduced to only 14% with a similar increase in flight range.[30]

Fish Schools

Energy economy for swimming by fish has been suggested as a possible advantage to schooling. Increased energy savings would be advantageous by permitting faster swimming speeds during foraging and increasing range particularly for migration. The pattern of the school is hypothesized to be dependent on the undulatory movements of the fish which produce a thrust-type vortex street (reverse Kármán vortex street).[3,21,31]

A three-dimensional, inviscid flow model was developed by Weihs to determine the optimal configuration between fish in a school for energy conservation.[3,22] The model considered the structure of an infinite array of identical fish swimming in an oncoming flow. The fish were organized in discrete layers and in evenly spaced rows so that fish in the trailing row were staggered and centered between two fish in the leading row. The stationary position of the fish in the flow is maintained by the oscillatory sideways propulsive motions of the fish from its body and caudal fin. The propulsive motions produce the vortex wake in which the rate of change of momentum in the water is equal and opposite to the thrust which opposes the total drag on the body (Figure 1). The equality of thrust and drag is maintained as the fish swims at constant velocity.

Considering only one layer of the theoretical school, the model predicted that the relative velocity directly behind a fish would be high, whereas the relative velocity would be lowest outside the vortex street.[3,21,22,31,32] Because the vortex wake takes time to fully develop and then dissipate further downstream, the optimal configuration is a diamond or shallow rhombus pattern with a leading fish, two fish in the second row, and a fish in the third row (Figure 4). The angles within the pattern are 30” and 150°.[3]

The first row of fish swimming into undisturbed water will have the same relative and absolute velocities. Fish in the second row experience a relative velocity 40–50% of the free stream velocity and a reduction of the force generated for swimming by a factor of four to six.[3,22] However, the decrease in relative velocity is not maintained with each successive row due to destructive interference. The vortex wakes of two successive rows will cancel because the vortices from each row are in line and have opposite vorticity when the lateral distances between adjacent fish is twice the width of the vortex street. The third row thus encounters undisturbed flow and incurs no reduction in relative velocity and drag. The reduced relative velocity occurs with alternate rows. Integrated over the entire formation, the school will have only a 50% savings in energy of the second row.[3]

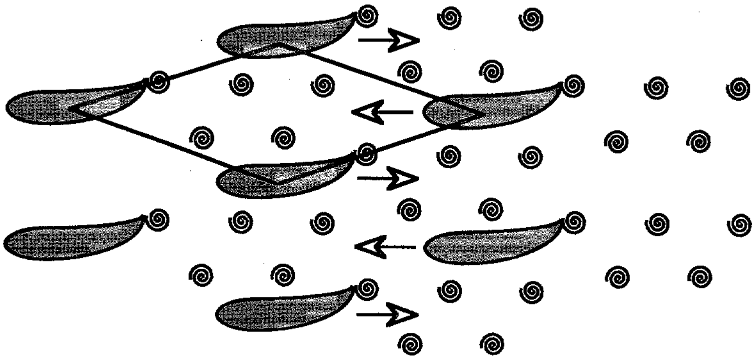

FIGURE 4 Optimal arrangement for maximum energy savings of a fish school swimming in a horizontal layer according to the model by Weihs.[3,22] Thrust-type vortex patterns in the wake of the fish are illustrated. Arrows show direction of induced flow relative to vortices. The diamond configuration of fish is shown by the solid lines.

Individual fish in alternate rows not experiencing reduced drag from the interaction of the vortex wake of the previous row may still contract a benefit from effects due to lateral spacing. As spacing decreases there is a channeling effect so that the force produced by a fish in a row may be twice that of a single fish.[22] The channeling effect is not added to the energy savings of the row encountering the effects of the vortex wake. The two effects may not be superimposed, because the trailing row has a reduced relative velocity which decreases lateral interactions.

In addition, Weihs has suggested that tip vortices from the pectoral fins could be exploited for lift by trailing fish.[3,22] Fish such as tuna are negatively buoyant and maintain trim from lift generated by the pectoral fins. Vorticity from leading fish would provide an upwash which would benefit trailing fish, analogous to the mechanism used by birds (see above).

The three-dimensional complexity of fish schools has made data collection to validate the model difficult. Schools of 20–30 individuals of saithe (*Pollachius virens),* herring (*Clupea harengus)* and cod *(Gadus morhua)* were tested in a circular tank.[33] Although the fish generated vortices in their wake as predicted by Weihs, the schools were not organized according to the model. In all cases the fish exhibited non-random spacing but did not mimic the optimal configuration predicted by Weihs' model. Trailing fish often swam with their snout ahead of the tail of the leading fish. Despite the lack of data supporting energy reductions by trailing fish, the observed lateral separation was about 0.9 body length and could still provide a 35% reduction in energy.

Observations on scombrid and salmonid fish do support the configuration predicted from the model. Jack mackerel (*Trachurus symmetricus)* and pink salmon *(Oncorhynchus gorbuscha)* swam in formations which approximated the diamond shape.' [34] Estimates of lateral distance by scombrids show relatively narrow spacings of less than one body length in which propulsive force is increased. Pacific mackerel *(Scomberjaponicus)* and bluefin tuna *(Thynnus thynnus*) in schools had lateral distances of 0.4–0.6 body length.[31,35,36]

Maximum duration of fish swimming in schools is 2–6 times longer than for a single fish,[30] which suggests energy economy and reduced metabolic effort. Oxygen consumption by fish schools were reported to be significantly lower than the collective consumption of an equivalent number of solitary fish, although this has been attributed more to group effect than to formation swimming.[31,37] To remove the group effect, three fish were tested as a school in a water current of 0.07 m/s.[38] Oxygen consumption was measured for the entire school and on individuals separated from the other two by a clear partition so as to maintain visual contact without experiencing flow distortion. **A** 13% reduction in oxygen consumption was found for the school compared to the sum for the individual fish. However, only schools of large individuals (approximately 60 mm in length) demonstrated measurable energy savings and the small diameter (50 mm) of the test chamber may have introduced errors due to blocking and wall effects.

Indirect measures of energy economy of fish schools are based on the kinematics of propulsive movements. Tail beat frequency was demonstrated to be lower for some individuals of Pacific mackerel ***(Scomber** japonicus)* when schooling than when swimming alone.[39] Fish such as mackerels beat their tails continuously when swimming; however, many fish swim intermittently using a burst-and-coast strategy.[8,40,41] In burst-and-coast swimming, the fish realizes an energy savings by decreasing its drag during the coast phase. **A** lower total energy expenditure to travel a given distance thus is achieved when compared to a fish which is constantly undulating over the same distance. Drag on an undulating fish body is 3–5 times higher than if the body is held straight and rigid.[42,43]

When three fish were examined swimming in the formation predicted by Weihs[3,22] for energy savings, the lead fish had equivalent mean times for bursting and coasting with solitary fish; whereas, the trailing fish demonstrated a reduced burst time and an increased coast time.[8] Coast time for trailing fish was 58 and 115% greater than coast time for leading and solitary fish, respectively. Coast and burst phases of trailing fish were nearly equal in duration. An energy reduction of 29 and 21% was estimated for the trailing fish relative to solitary fish swimming continuously and leading fish, respectively. Although the combination of formation swimming and burst-and-coast strategies allows for increased energy savings, the simultaneous use of both behaviors reduces the effectiveness of either strategy alone. The interaction of the two strategies would negate attainment of the optimal configuration, because as the trailing fish coasts it moves backward relative to the leading fish. The trailing fish must then accelerate to return to its original position. In addition, coasting by a leading fish does not generate the vortex pattern exploited by trailing fish. Such conditions may explain the deviation in natural formations from the model.[8,33]

Although the drag-type Kármán vortex pattern in the wake of a bluff body is the best known of the vortex systems described above, there has been no theoretical analysis of this system with respect to energy economy in formation travel. All analyses of this system have been performed experimentally.

The most readily identifiable example of using a single-file formation to lower energy costs is associated with automobile racing. Tests on model race cars in a wind tunnel suggest that a race car drafting another could reduce its drag by 37%.[7] This effect occurs when the separation distance between cars is 1.1 car lengths, but the effect diminishes with increased separation. A car immediately behind another is assisted by the low pressure developed in the rear position of the leading vehicle.[44] Since the lead car also experiences a reduction in drag from modification of the pressure distribution, two or more cars working together can increase their top speed.[45] Four cars moving in single-file experience reduced drags with spacings less that one car length.[46]

Even when internal combustion engines are exchanged for biological engines in mechanical systems, the drafting effect still permits enhanced performance. Cyclists will travel in pace lines whereby each cyclist travels closely behind another. A greater drag reduction occurs the more closely one cyclist follows another.[6] Drafting cyclists experience a 26–35% energy savings in a pace line (Figure 5).[5,6] Greater energy savings are obtained when cyclists follow in a pack (39%) or when drafting behind a more massive body (62%), such as an automobile.[5,6,47] This latter drafting technique allows for an increase in performance far beyond the capabilities of a single cyclist, whereby cycling speeds of over 220 km/hr have been achieved.[48]

Reduced metabolic effort was demonstrated for tandem human runners.[49] By running close behind another, 80% of the oxygen consumption required to overcome the air resistance was eliminated by running at 6 m/s behind another runner. Because the energy cost in overcoming air resistance is 7.5% of the total energy cost of running, a following runner can increase speed above the maximum speed corresponding with the maximum oxygen consumption by 6%.

In nature, single-file formations to reduce transport cost occur regularly. These formations or queues are used during the autumnal mass migratory

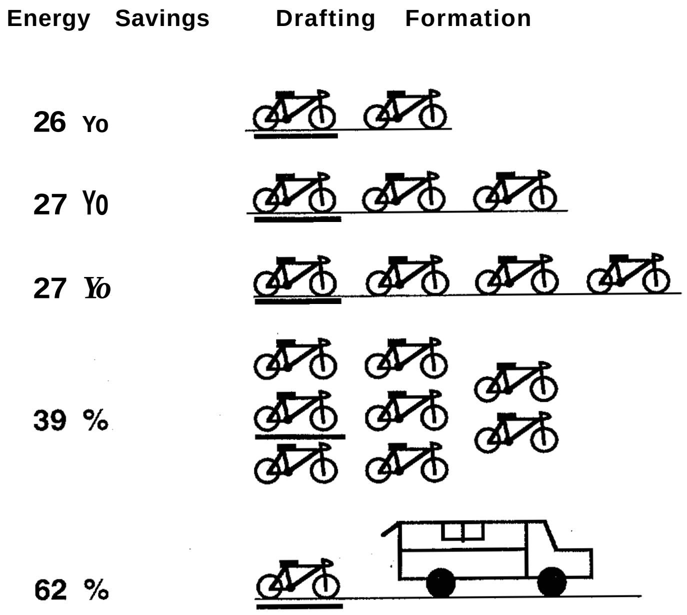

FIGURE 5 Reduction of metabolic rate of cyclists drafting in different formations at 11.2 m/s.[5] The underlined bicycle represents the position from which measurements were obtained. Redrawn from Hagberg and McCole.[5]

movements of the spiny lobster, *Panulirus argus*.[18] The lobsters walk along the ocean bottom for periods of several days in queues of up to 65 individuals with a tight spacing maintained by tactile contact. Although single-file terrestrial movements by caribou are reported to lower energy demands by packing down snow,[50,51] the benefit to walking in queues by lobster results from flow modification in the aquatic environment.'' Experimental measurements of drag on individual lobsters organized in line formations indicated increased energy economy and locomotor performance. Queues sustained less drag per individual than single lobsters traveling at the same speed. The reduction in the energetic cost per individual in a queue was a direct function of speed and queue size. A queue of 19 lobsters moving at 3.5 m/s had a 65% lower drag than when the lobsters were tested individually, but there was only a 10% energy savings at a slower velocity of 1.5 m/s. In addition, queues composed of large numbers of lobsters had lower drags per individual than queues of smaller number.

For ducklings, traveling behind the mother duck provides an opportunity to take advantage of the vorticity in the wake.[10,19] When mallard ducklings *(Anus platyrhynchos)* were imprinted to follow an adult decoy in a water flume at 0.3 m/s, the ducklings followed in discrete formations (Figure 6) with interduckling distances typically less than one-quarter body length.[10] Metabolic rate per individual decreased with increasing clutch size by 7.8–43.5% (Figure 7).[19] Ducklings swimming directly behind the decoy showed a 37.7, 27.6 and 15.7% decrease in their metabolic rate relative to swimming without the decoy at 3, 7, and 14 days of age. Maximum individual energy savings of 63% were realized by four 3-day-old ducklings swimming in the decoys wake. Even

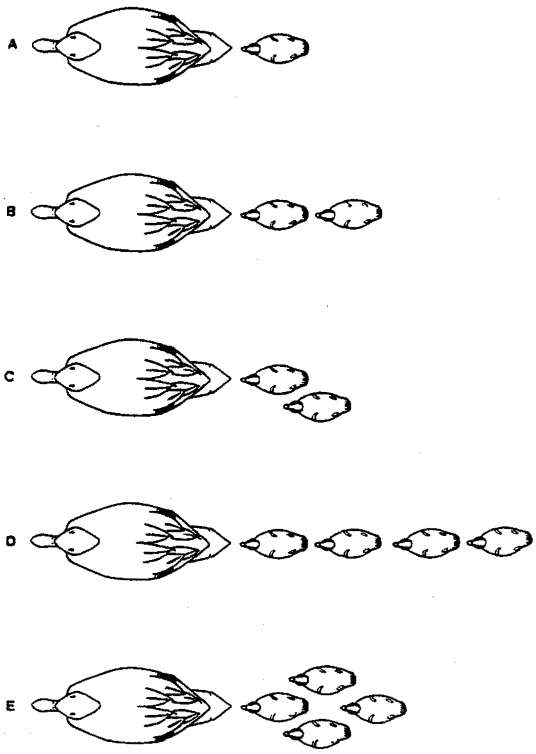

FIGURE 6 Typical duckling formations for clutches of one, two, and four individuals. Single-file formations are shown in **A,** B and D; echelon formation is shown in ***C;*** diamond formation is shown in E.

without the decoy, the ducklings were able to draft off one another. These energy savings were further expressed in the duckling's cost of transport (energy used to move a unit mass a unit distance). The 3-, 7-, and 14-day-old ducklings swimming in four-duckling clutches in the decoy's wake reduced cost of transport by 66.3, 49.6, and 32.1%, respectively.

Observations of kinematic movements of the paddling feet revealed that the ducklings in the most posterior positions attained the greatest energetic savings.'' Stroke frequency remains constant at different swimming velocities in mallard ducklings, but amplitude of the stroke, expressed as length of the arc traversed by the foot, increases with respect to increasing velocity.[10,51] Thus, ducklings encountering a lower relative velocity in the wake of the decoy or other ducklings will have shorter arc length than ducklings unaffected by vorticity. Generally, larger formations showed the greatest reduction in arc length (Figure 8). Compared to a solitary duckling, trailing ducklings demonstrated paddling arc lengths that were 15.6–29.8% lower when in the decoy's wake.'' Although also demonstrating a reduced arc length, leading ducklings showed only a 4.7–22.6% decrease.

That the most posterior individual in a single-file formation obtains the greatest energetic benefit is supported by positional data from cars and

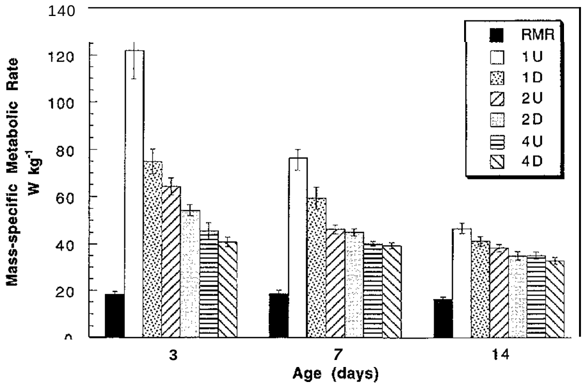

FIGURE 7 Mass-specific metabolic rates (± SE) of ducklings imprinted to swim behind a decoy while in a water flume. Swimming velocity was 0.3m/s. Ducklings were tested at ages of 3, 7, and 14 days. Combinations **of** clutch size (1, 2, and 4 ducklings) and decoy position (U, up above the water surface; D, down in the water) are displayed in the insert. Resting mass-specific metabolic rates are indicated by RMR in the insert. Figure is from Fish.''

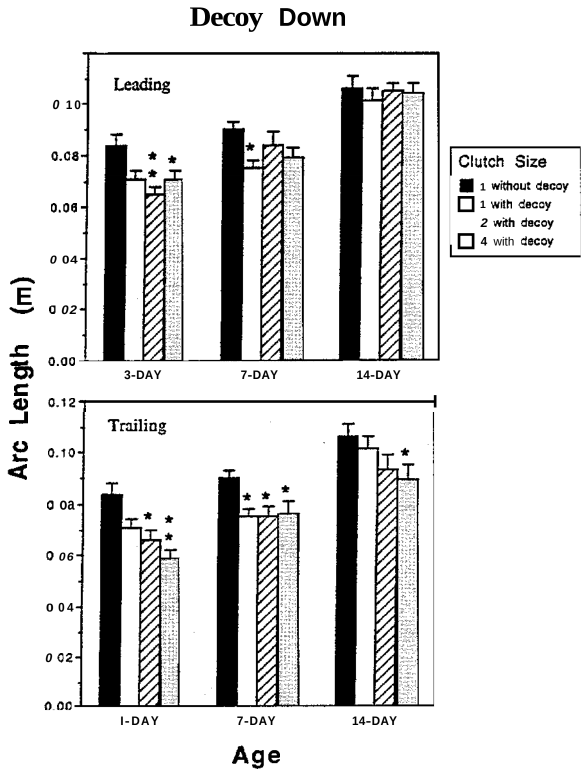

FIGURE 8 Comparison of arc length traversed by the paddling feet of different aged ducklings at leading and trailing positions in formation swimming behind an adult decoy. The solid bar represents means (± SE) for solitary ducklings swimming without the aid of the decoys wake; whereas, the other bars represent means (± **SE)** for ducklings swimming in the decoys wake. Asterisks indicate significant differences ($^*P < 0.05$; $^{**}P < 0.01$) between ducklings swimming in the decoy's wake and a solitary duckling. Figure is from Fish."

cyclists. The trailing vehicle in a four-car platoon had the lowest drag which was *62%* of a car that was not drafting.[46] Cyclists incur low drag in the most posterior position in a pace line.[5,6] According to Kyle (pers. comm.), drag is reduced the farther a rider is from the leader. Relative to a solo cyclist, a 2% reduction in wind resistance is experienced by the rider in the first position of a pace line, 42% by the second rider, 52% by the third rider, and 53% by the rider in the fourth position.

CONCLUSION

The use of vortex theory has broadened our understanding of the dynamics of animal locomotion and material transport in air and water.[20,53–57] Vortices are used by animals during locomotion to improve performance in thrust and lift generation, increase efficiency, and reduce drag.[56–59] The flow regime established by the vortex pattern of animals moving in formation can be exploited for energy economy. Maximum energy savings of 50–60% may be achieved by trailing individuals within a formation with lower but significant savings averaged over the entire formation.[3,5,11,19] The vortex wakes reduce the relative velocities for trailing animals arranged in particular positions within a formation depending on the mechanism of vortex generation. Optimal configurations include V or echelon formations with wing tip vortices, staggered diamond formations with thrust-type reverse Kármán vortex systems, and single-file formations with drag-type Kármán vortex streets.

Effective positioning for energy conservation within a formation requires an ability to detect changes of velocity from the flow field of the leader. In fish, the lateral line could provide the ability to detect water flows from other individuals within a school. Schooling fish demonstrate low response latencies to stimuli from acoustico-lateralis input irrespective of visual sensory input.[60] Sensory information from the flow field of flying animals is detected similarly by mechanoreceptors. Tactile cephalic hairs on locusts may detect rhythmic changes in wind speed, wind direction, turbulence or a combination of these stimuli permitting coordination of wing beat between individuals.[61] Coordination between two locusts flying in tandem increases lift generated by the rear locust which may confer a possible energetic advantage to that individual. Mechanoreceptors on or near feather follicles in the wing can measure airspeed[62] which is prerequisite for precise positioning to achieve energy savings in flight formations. The ability to sense velocity changes due to shed vorticity could aid in synchronizing propulsor oscillation to enhance energy extraction by members of a formation.[59] However, animals travelling in groups seldom coordinate their propulsive movements.[8,25,61,63]

An understanding of the mechanics and energetics of formation movement however can not resolve all explanations of this behavior. Deviation from optimal formation configurations for energy economy[8,16,17,25–29] suggest that maintaining precise position may be difficult due to the reception of sensory stimuli and associated response times between individuals,[9,35] and that other benefits also may influence a organized gregarious behavior.[1–4,9 18,19,38] Despite these benefits, the proportion of an animal's overall energy budget associated with locomotion is high[41] and use of formation travel represents an important energetic strategy to reduce these costs.

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