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Chapter 13

Energy conservation by formation swimming: metabolic evidence from ducklings

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Formation movement, particularly during swimming and flying, has been hypothesized to reduce an individual animal's energy expenditure. Although a number of aerodynamic and hydrodynamic models have been proposed to estimate energy savings of animals travelling in formation, little empirical data are available that test this presumption. An examination of the metabolic energetics of formation swimming was undertaken with mallard ducklings (*Anus platyrhynchos*) trained to swim behind a decoy in a flow tank. Oxygen consumption was measured for ducklings in clutches of one, two or four individuals, with the decoy in the water or suspended above the surface. Metabolic rate per individual duckling decreased with increasing clutch size by 7.8-43.5%. Following in the wake of a decoy significantly decreased metabolic swimming effort by ducklings and this effect was most pronounced at three days of age and in small clutches. These findings suggest that the flow pattern generated by the formation and in the wake of an adult reduces the resistance of the water to locomotion and allows an individual duckling to conserve energy.

INTRODUCTION

Locomotion is an energetically costly activity that may comprise a significant component of an animal's overall energy budget (Weihs & Webb, 1983; Fish, 1992). Therefore it is advantageous for animals to use locomotor strategies which minimize energetic expenditure. Such strategies include gait transition, intermittent locomotion, soaring, tidal stream transport, wave riding, submerged swimming, porpoising and formation movement (Cone, 1962; Lissaman & Schollenberger, 1970; Pennycuik,

1972; Weihs, 1973, 1974, 1978; Au & Weihs, 1980; Hoyt & Taylor, 1981; Williams, 1989; Fish *et al.*, 1991; Williams *et al.*, 1992).

Formation movement by animals has been hypothesized to reduce energy expenditure and enhance locomotor performance of individuals during walking (Fancy & White, 1985), swimming (Weihs, 1973; Breder, 1976), and flying (Lissaman & Schollenberger, 1970; Hummel, 1983). Saving energy by moving in formation has been suggested as particularly important for animals that migrate by swimming or flying over considerable distances. Formation swimmers or flyers influence the flow of water or air around adjacent individuals in formations, thereby presumably reducing drag with a concomitant decrease in the overall energy cost of locomotion.

As a mechanism for energetic reduction of locomotor effort, formation movement is accepted generally for automotive and cycling competitions, which use the techniques of 'drafting' or 'slipstreaming'. Trailing cyclists in a pace line experience a 38% reduction in wind resistance and 35% reduction in power output (Kyle, 1979). Reduced metabolic effort of 6.5% has even been measured in the trailing human runners (Pugh, 1971).

Energy savings have been difficult to measure for animal locomotion. The three-dimensional complexity and large size of polarized animal formations, such as fish schools and V formations of geese, have deterred metabolic experimentation to evaluate hypotheses of energy savings by formation movement (Breder, 1976; Shaw, 1978; Hummel, 1983).

Vorticity and relative velocity

The physical basis for energy savings with formation flying and swimming is that as a body moves through a fluid it distorts the velocity field around the body and in its wake. The wake consists of a trail of alternating vortices which are regularly arranged as two staggered rows (Prandtl & Tietjens, 1934; Vogel, 1981; Weihs & Webb, 1983). The vorticity transports momentum within the fluid and affects the velocity profile. Each vortex induces velocities in the surrounding fluid in the same direction as the rotation of the vortex (Weihs & Webb, 1983). The strength of the induced velocity is inversely proportional to the distance from the vortex. Changes in the velocity profile of the fluid influence the relative velocity of trailing bodies in the wake (Breder, 1965, 1976; Belyayev & Zuyev, 1969; Weihs, 1973, 1975). Relative velocity is calculated as the difference between the trailing body's velocity and the mean velocity induced by the vortices shed from the leading body (Weihs, 1973). If a trailing body is moving at a given velocity, and oriented in the same direction as the mean velocity of the vorticity shed into the wake by a leading body, the trailing body will experience a reduction of its relative velocity. Because drag is directly proportional to the velocity squared, a decrease in the relative velocity can decrease drag. A lower drag would require a reduced energy expenditure to generate thrust, which is equal to the drag for steady swimming.

The benefit of travelling in the vortex trail of another body depends on the relative position of the bodies and the mechanism of vortex generation (Figure 1). An oscillating body, such as a swimming fish, generates a thrust-type vortex trail (Figure 1A;

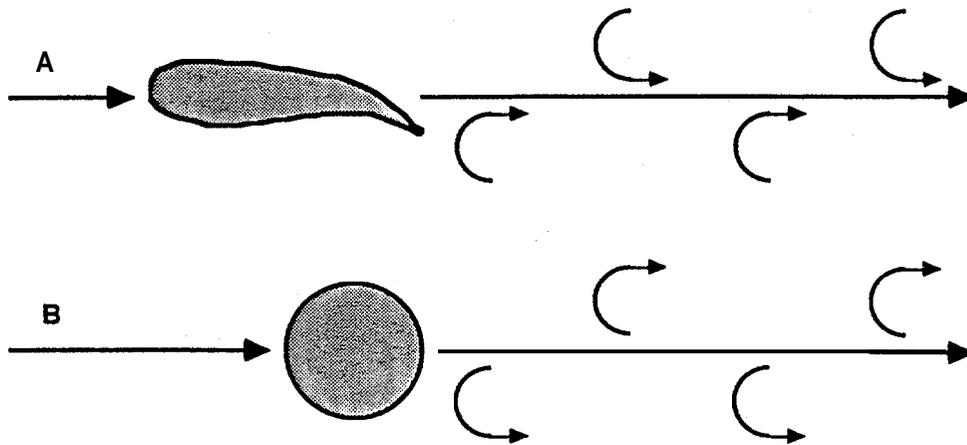


Figure 1. Two-dimensional flow patterns generated in the wake of a body. Arrows indicate direction of flow relative to the body. The thrust-type vortex trail (A) is actively produced by the periodic lateral oscillations of a fish (Weihs, 1972). The drag-type wake of a rigid body (B) has a pattern of vortices that rotate in the direction opposite to the thrust-type vortex trail.

Weihs, 1972). Owing to the rotation of the vortices, a low relative velocity and high energetic advantage are experienced by a fish swimming diagonally behind another fish (Weihs, 1973). Conversely between Reynolds numbers of 4×10^4 and 2×10^5 , the rotation of vortices induced by a rigid body is the reverse of vortices generated by lateral oscillations of fish (Figure 1B; Prandtl & Tietjens, 1934; Hoerner, 1965; Weihs, 1975; Vogel, 1981). The flow regime in this drag wake would produce a low relative velocity directly behind a rigid body. In this case animals moving in a single-file formation will experience reduced drag and energy expense. In addition, the vortex pattern behind a rigid body is such that momentum flows towards the body (Rayner, 1985), and a trailing body can be pulled along as momentum is transferred to it from the water. Young animals swimming in the drag wake of a larger adult will benefit particularly from this effect.

Predictive Models

Previous analyses of energy savings by formation movement in animals have focused on aero- and hydrodynamic models (Lissaman & Shollenberger, 1970; Weihs, 1973, 1975; Higdon & Corrsin, 1978; Badgerow & Hainsworth, 1981; Hummel, 1983). These models predict significant energy savings when animals are arranged in appropriate formations. Lissaman & Shollenberger (1970) estimated a 71% saving of induced power for birds flying in V formations.

A three-dimensional, inviscid, hydrodynamic model for fish schools developed by Weihs (1973, 1975) estimated reductions of swimming effort by a factor of five for fish swimming in diamond-shaped formations. Trailing fish in these formations take advantage of vortex trails produced by leading fish. The relative velocity of the trailing fish is estimated at 40-50% of the free stream velocity.

Observations on bird flocks and fish schools indicate, however, that individuals often deviate from the optimal configuration (Partridge & Pitcher, 1979; Badgerow & Hainsworth, 1981; Hainsworth, 1987; Fish *et al.*, 1991). Thus for animals moving in groups, energy savings may be lower than the maximum predicted, and the energetic cost of travel may even be greater than for a solitary individual.

Experimental measurements on formations

Little empirical data are available that test the presumption of energy economy by formation swimming. Fish in schools were reported to swim 2-6 times longer than single fish (Belyayev & Zuyev, 1969). Examinations of swimming kinematics of fish schools indicate energy savings by increasing coast times during burst-and-coast swimming (Fish, *et al.*, 1991) and reduced tail-beat frequency (Fields, 1990). Abrahams & Colgan (1985) measured respiratory rates of schools of three fish swimming in a water current of 0.07 m s^{-1} . Fish were tested as a school and in groups of two separated by a clear partition. A 13% reduction in respiratory rate of the school was found compared to the sum for individuals. However, only schools of large individuals (6 cm length) demonstrated measurable energy savings and the small diameter (5 cm) of the test chamber may have introduced errors due to wall effects.

Queues of spiny lobsters (*Panulirus argus*) in water have been shown to sustain less drag per individual than a single lobster travelling at the same speed (Bill & Herrnkind, 1976). The reduction in energetic cost per individual in a queue was a direct function of queue size. Queues composed of large numbers of lobsters had lower drag per individual than queues of smaller numbers. Drag reduction for individual lobsters was suggested to be important in conserving energy during migration when these animals form queues.

Formation swimming by ducklings

The paucity of empirical data to support or refute the hypothesis of energy conservation through formation movement in animals is a result partly of the cumbersome size of the formation and partly of uncontrolled and inconsistent positioning of individuals in the formation. Energetic measurements have been more forthcoming from studies of line formations in which a rigid body is responsible for the vorticity pattern (Bill & Herrnkind, 1976; Pugh, 1971; Kyle, 1979). Mallard ducklings are well suited for metabolic examination of formation swimming owing to their habit of swimming in single file. These ducklings display a following response due to imprinting on their mother (Hess, 1959; Dyer & Gottlieb, 1990; Bolhuis, 1991) and are capable of being led to water within 12 h of hatching (Bellrose, 1976). A fortuitous consequence of the single-file formation would be a reduction in metabolic effort during swimming, due to a decrease in their relative velocities associated with the wake and pattern of vorticity shed by the leading bodies.

One-day-old ducklings were imprinted on a female mallard duck decoy. The ducklings were trained daily to swim for 20-30 min at 0.3 m s^{-1} behind the decoy in the working section ($1.2 \times 0.6 \times 0.44 \text{ m}$) of a recirculating water channel (Vogel & LaBarbera,

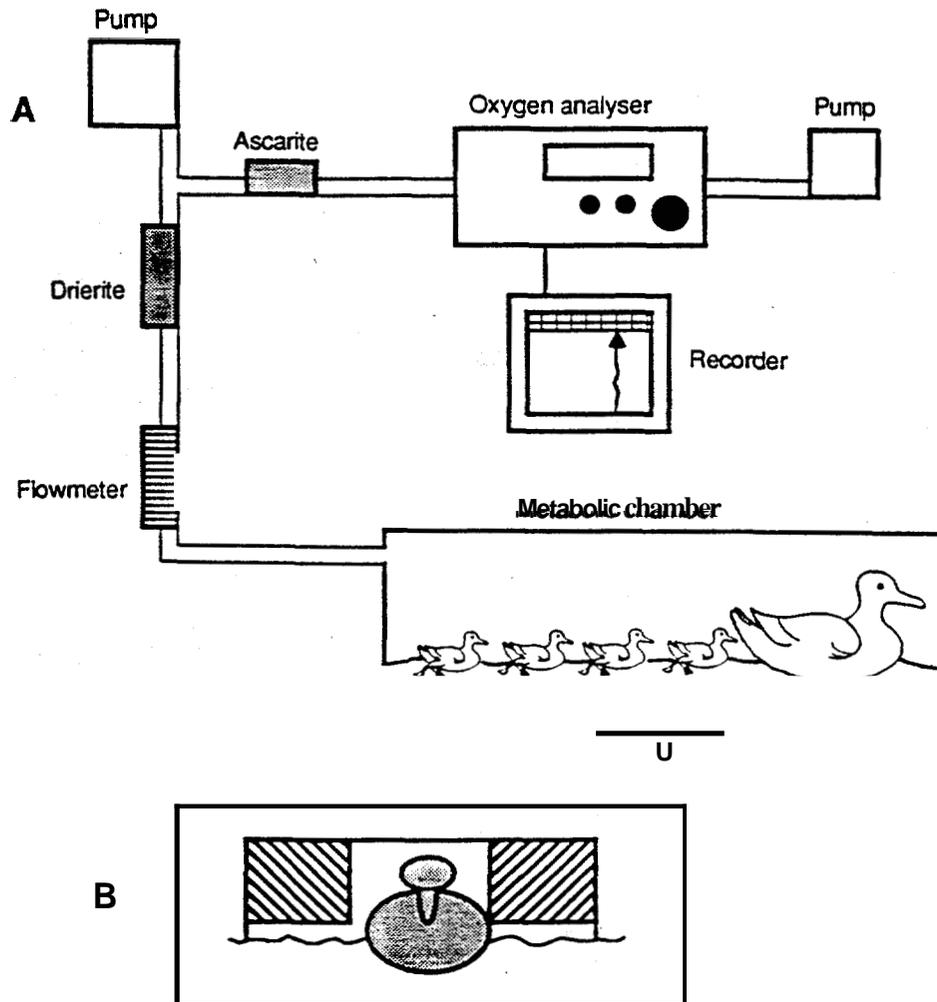


Figure 2. (A) Diagram of oxygen analysis system. (B) Insert shows cross-sectional view of metabolic chamber with decoy. Filled area represent dead-air spaces. Water velocity was controlled by two electric motors (Minn Kota 65MX). Water velocity was checked with either a mechanical propeller flow meter (KAHLISCO Model 005WB138) or electromagnetic flow meter (Marsh-McBirney Model 201). Mean water temperature was $21.6^{\circ}\text{C} \pm 1.0$ (SD).

1978). The upstream end of the working section was bounded by a plastic grid to reduce turbulence in the flow.

A Lucite metabolic chamber was fitted over the working section (Figure 2). The chamber provided a large enough space to allow ducklings to organize into formations and avoid interference with flow and wave patterns generated by the animals. Oxygen-content of dry, carbon-dioxide-free air flowing continuously through the chamber ($3\text{--}10\text{ l min}^{-1}$) was monitored with an oxygen analyser (Ametek S-3A/I; Figure 2). Metabolic rate (MR) was measured from oxygen consumption at STP calculated using equations for open circuit respirometry (Hill, 1972) and was expressed in kcal using a

caloric conversion factor of 4.8 kcal l⁻¹.

The position of the ducklings in formation and with respect to the decoy was monitored with a video camera. To videotape a dorsal view of the ducklings in the water channel, a mirror was suspended at a 45° angle above the working section.

Twelve groups of seven ducklings were examined. After imprinting, each group was subdivided into three experimental clutches of one, two, and four ducklings. Each experimental clutch was tested at 3, 7, and 14 days of age. The effect of the decoy's wake was determined by ducklings swimming with the decoy in the water or with the decoy raised approximately 0.01 m above the water surface. In the latter position, ducklings could maintain the visual cue of the decoy, but would not experience a wake generated by the decoy. Over a 2-d period, each clutch was tested with the decoy in the up or down position. The order of testing was assigned randomly. Mean masses for 3-, 7-, and 14-d-old ducklings were 0.054 kg ± 0.009 (SD), 0.109 ± 0.017 kg, and 0.243 ± 0.050 kg, respectively.

Metabolic results of ducklings information

Ducklings readily followed the decoy when swimming in the water channel (Figure 3). The Reynolds numbers for 3-, 7-, and 14-d-old ducklings, and the decoy were

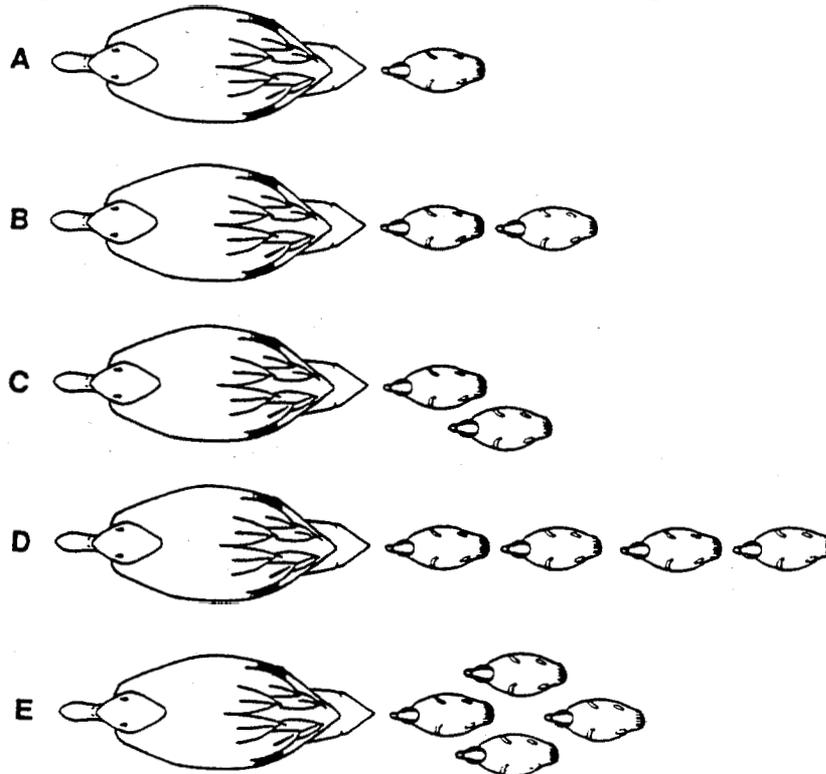


Figure 3. Typical duckling formations for clutches of one, two, and four individuals. Single-file formations are shown in (A), (B) and (D); echelon formation is shown in (C); diamond formation is shown in (E).

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2.15×10^4 , 2.82×10^4 , 3.60×10^4 , and 8.94×10^4 , respectively, based on waterline length. Solitary or leading ducklings maintained an average position of 0.25 body-lengths behind the 'decoy'. This distance was maintained regardless of whether the decoy was in or out of the water. Pairs of ducklings were in formations where they swam abreast, one behind the other, or one lateral and slightly behind the other. Clutches of four ducklings typically swam in single-file lines or in diamond-shaped formations. Inter-

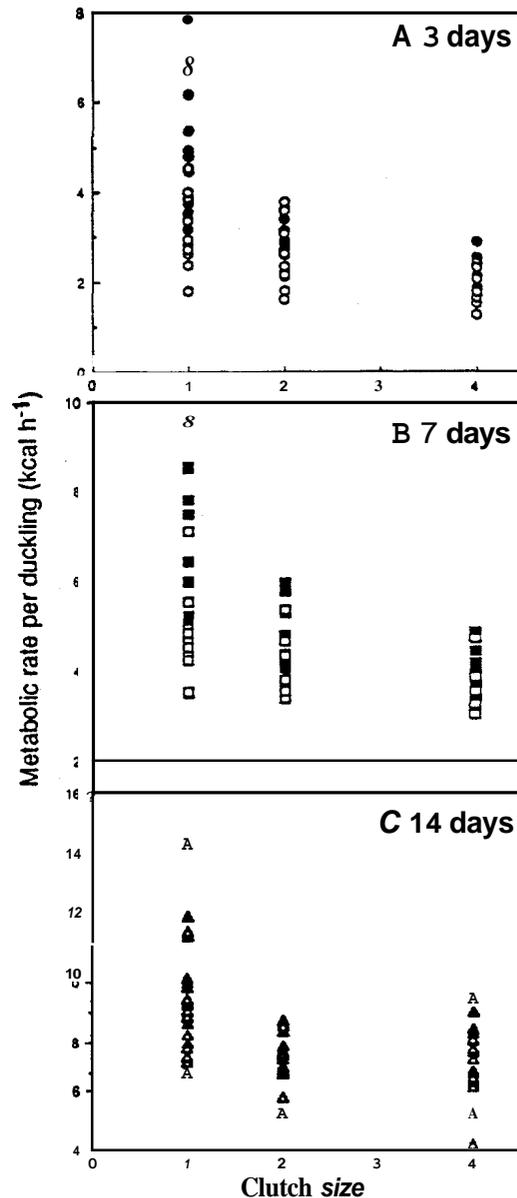


Figure 4. Metabolic rates of ducklings in clutches of one, two, and four individuals at ages of (A) 3 d, (B) 7 d and (C) 14 d, while swimming downstream of a decoy. Closed symbols represent clutches following a decoy suspended above the water surface; open symbols represent clutches following a decoy that is producing a wake in the water.

duckling distances were small and averaged 0.1 body lengths. Ducklings would reposition themselves frequently throughout the testing period.

Metabolic data showed increasing energy economy with increasing clutch size and with influence of the decoy's wake (Figure 4). Significant differences (ANOVA, $P < 0.001$) were found with respect to age, decoy position, clutch size, and interaction of decoy position with clutch size. Metabolic rate per duckling decreased by 7.8-43.5% with increasing clutch size for all age classes and decoy positions. The best performance with regard to energy economy was found for 3-d-old ducklings. These ducklings displayed a 62.8% decrease in metabolic effort when swimming in a clutch of four in the decoy's wake compared to a solitary duckling without the decoy's wake. Duckling clutches of one were significantly different (SNK, $P < 0.05$) from all other clutches regardless of age or decoy position.

Reduced metabolic effort due to the influence of the decoy's wake was most important in the youngest ducklings. Solitary 3-d-old ducklings showed a 37.7% decrease in MR when swimming in the decoy's wake as opposed to 27.6 and 15.7% decreases for solitary 7- and 14-d-old ducklings, respectively. However as clutch size increased, the influence of the decoy was less pronounced, showing only 7.5-13.1% decrease in MR.

Equivalent results were found when using mass-specific MRs, which were calculated as the clutch MR divided by the total mass of the clutch (Figure 5). The swimming ducklings had mass-specific MRs 2.0-6.6 times the resting MR over the range of ages. Significant differences (ANOVA, $P < 0.005$) were found with respect to age, decoy

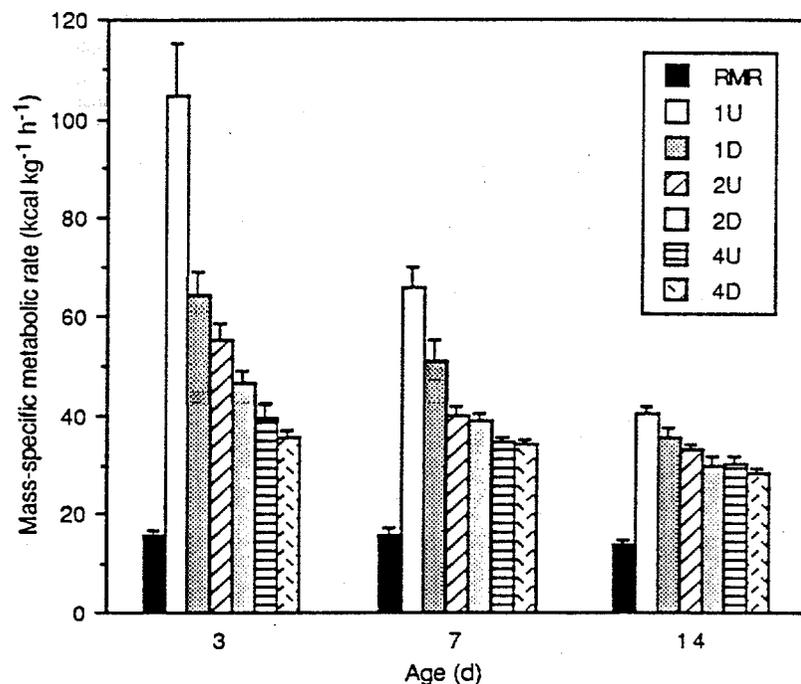


Figure 5. Mass-specific metabolic rates (\pm SE) of ducklings at ages of 3, 7, and 14 d. Combinations of clutch size (1, 2, and 4 ducklings) and decoy position (U, up above the water; D, down in the water) are shown in the insert. Resting mass-specific metabolic rates are indicated by RMR in the insert.

position, clutch size, and all interactions. Ducklings following in the decoy's wake realized a saving of 20% (SNK, $P < 0.05$; all clutch sizes and ages combined) compared to ducklings swimming with the decoy in the raised position. With all ages and decoy positions combined, mass-specific MR decreased by 33% between clutches of one and two ducklings, and by 18% between clutches of two and four ducklings (SNK, $P < 0.05$).

Cost of transport

The importance of energy economy by formation swimming for young ducklings is apparent when the cost of transport (CT) is examined. The cost of transport (CT) was calculated from the mass-specific metabolic rate divided by swimming velocity (Schmidt-Nielsen, 1972; Tucker, 1975). The 3-, 7-, and 14-d-old ducklings swimming in four-duckling clutches in the decoy's wake reduced CT by 66.3, 49.6, and 32.1%, respectively (Figure 6). Despite the large reductions in CT, ducklings were found to have the highest CT for any vertebrate swimmer (Schmidt-Nielsen, 1972; Tucker, 1975; Fish, 1992). Solitary 3-d-old ducklings had a CT 88.8 times greater than the minimum CT of a fish of equivalent size, and 17 times greater than an adult mallard duck (Figure 7). These high costs for young ducklings are due probably to scale effects associated with (a) their high maintenance costs of homeothermy in water, (b) their increased drag at the water surface from wave formation, and (c) the inefficiency of their paddling mode (Fish, 1982, 1992; Baudinette & Gill, 1985).

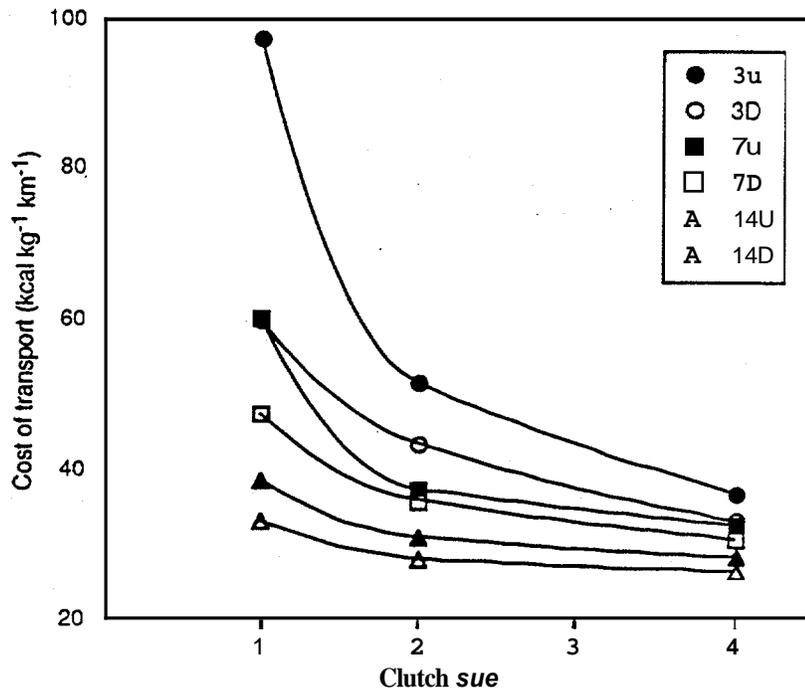


Figure 6. Comparison of costs of transport for clutches of different numbers of individuals. Values were based on mean mass-specific metabolic rates. The insert shows symbols for combinations of the age in days of the ducklings (3, 7, 14) and the position of the decoy (U, up above the water; D, down in the water).

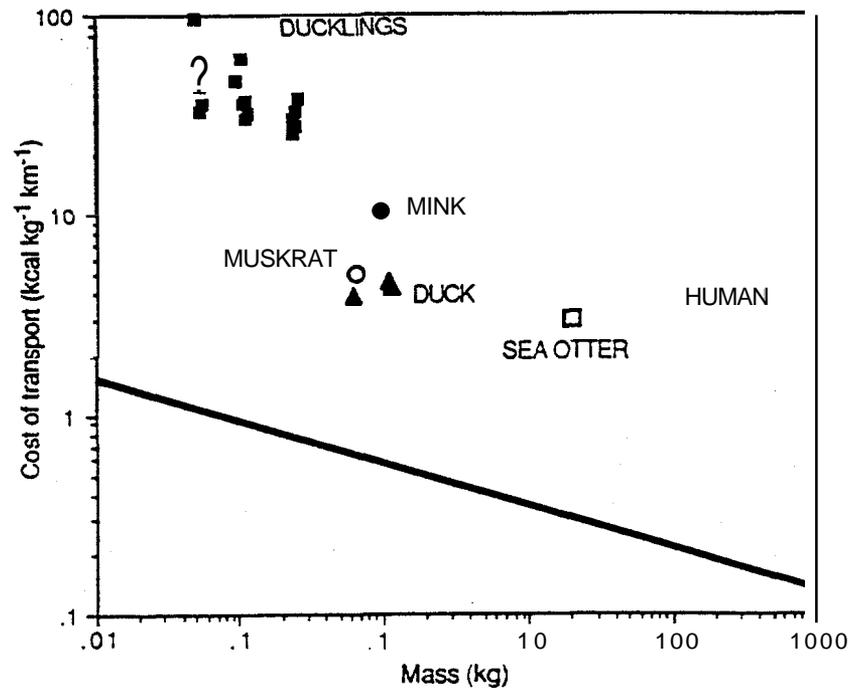


Figure 7. Cost of transport of ducklings compared with other swimmers. Other surface paddlers include duck (Prange & Schmidt-Nielsen, 1972; Woakes & Butler, 1983; Baudinette & Gill, 1985), human (Di Pramero, personal communication, 1979), mink (Williams, 1983), muskrat (Fish, 1982), and sea otter (Williams, 1989). The solid line is the minimum cost of transport extrapolated from data on fish (Davis *et al.*, 1985).

DISCUSSION

Although ducklings experience increased energy economy when swimming in formation, it should be cautioned that other reasons may have led ultimately to this behaviour. Formation movement by various animal species has been related to protection against predation, locating food resources, mating efficiency, pooling orientation information, greater tolerance to toxic substances and increasing energy economy (Brock & Riffenburgh, 1960; Breder, 1967, 1976; Weihs, 1973; Shaw, 1978; Hummel, 1983). Formation movement by ducklings is advantageous where swimming performance is potentially limited by energy availability. A reduction in energy expenditure and drag during formation swimming would allow ducklings as a group to swim for longer durations and at higher speeds than as individuals.

Limitations on performance on ducklings may be severe, because of their swimming mode. Surface swimming by ducklings is accomplished by using alternate strokes of the webbed hind feet in a paddle-propulsive mode. Although repetitive paddling is used at slow speeds and for surface swimming, this mode is uneconomical due to its high drag and corresponding inefficiency (Prange & Schmidt-Nielsen, 1970; Fish, 1982, 1984b, 1992; Baudinette & Gill, 1985; Stephenson *et al.*, 1989).

Swimming at the water surface can limit performance by increasing the drag experienced by the body due to an additional wave drag component. Wave drag can increase total drag by a factor of five (Hertel, 1966). In addition, maximum cruising speed is limited by interaction of waves created by the body. The maximum sustainable speed of mallard ducks (Prange & Schmidt-Nielsen, 1970) and muskrats (Fish, 1982) coincided with their predicted hull speeds based on the performance of surface craft. Hull speed is the practical limit to the speed of a displacement hull at the water surface due to the increased drag from wave formation. Hull speed is dependent on the waterline length of the body, so that hull speeds for small bodies are lower than for large bodies. The configuration of duckling formations may effectively increase the waterline length for the entire clutch and allow ducklings to achieve higher sustained swimming speeds as a group than individually.

The reduced energy economy associated with increasing age of the ducklings indicates the importance of inertial effects in formation swimming. When dye was injected behind the decoy, the rotation pattern of the vortices was similar to the condition illustrated in Figure 1B. The momentum transported in the water by the vorticity could be imparted to the trailing ducklings. Because momentum is directly proportional to mass, for a given amount of momentum transferred a smaller duckling will be more effectively pulled along behind the decoy than a larger duckling. This was observed particularly when comparing the metabolic effect on single ducklings swimming with or without the wake of the decoy. The energy saving by 3-d-old ducklings in the decoy's wake was over twice as great as for a 14-d-old duckling which was 4.5 times the mass. A similar situation is observed in porpoises where a smaller animal, often an infant, positions itself close to and slightly behind a larger porpoise to obtain a free ride (Norris & Prescott, 1961). In motor pacing, a human cyclist drafts behind a more massive body such as an automobile and achieves speeds over 220 km h⁻¹ (Gross *et al.*, 1983).

In addition to the beneficial vortex pattern established in the drag wake of the decoy, the thrust wake produced by the paddling movements of the ducklings feet may aid in reducing swimming costs. As a foot is swept posteriorly during the power phase of the paddling stroke, a pair of vortices will be generated with one vortex located directly above the other (Alexander, 1982). The rotation and position of the upper vortex is such that it could transfer momentum and reduce the relative velocity of a trailing duckling. This effect could be even larger for ducklings swimming in the thrust wake of an actively paddling adult.

Energy saved during formation swimming could maximize the net rate of energy gain by making more energy potentially available for growth and other functions. Mallard ducklings experience their highest mortality within 18d of hatching (Orthmeyer & Ball, 1990). Attainment of adult body size through an increased growth rate benefits individuals by decreasing predation risk, increasing thermoregulatory control, and increasing locomotor performance. The latter point is especially critical for migrating birds that must reach full flight capability in time for autumn departure.

In conclusion, formation movement by ducklings reduces metabolic effort during swimming. The influence of following in the wake of a decoy significantly decreased

metabolic swimming effort by ducklings, and was most pronounced for the youngest ducklings and small clutches. **These** findings suggest that the **flow** pattern generated by the formation reduces **the** drag encountered when swimming and allows for conservation of energy **on an** individual **basis**.

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REFERENCES

- Abrahams, M.V. & Colgan, P.W., 1985. Risk of predation, hydrodynamic efficiency and their influence on school structure. *Environmental Biology of Fishes*, **13**, 195-202.
- Alexander, R.McN., 1982. *Locomotion of animals*. Glasgow: Blackie.
- Au, D. & Weihs, D., 1980. At high speeds dolphins save energy by leaping. *Nature, London*, **284**, 548-550.
- Badgerow, J.P. & Hainsworth, F.R., 1981. Energy savings through formation flight? A re-examination of the vee formation. *Journal of Theoretical Biology*, **93**, 41-52.
- Baudinette, R.V. & Gill, P., 1985. The energetics of 'flying' and 'paddling' in water: locomotion in penguins and ducks. *Journal of Comparative Physiology*, **155B**, 373-380.
- Bellrose, F.C., 1976. *Ducks, geese and swans of North America*. Harrisburg, Pennsylvania: Stackpole.
- Belyayev, V.V. & Zuyev, C.V., 1969. Hydrodynamic hypothesis of school formation in fishes. *Problems of Ichthyology*, **9**, 578-584.
- Bill, R.G. & Herrick, W.F., 1976. Drag reduction by formation movement in spiny lobsters. *Science, New York*, **193**, 1146-1149.
- Bolhuis, J.J., 1991. Mechanisms of avian imprinting: a review. *Biological Reviews of the Cambridge Philosophical Society*, **66**, 303-345.
- Breder, C.M. Jr, 1965. Vortices and fish schools. *Zoologica*, **50**, 97-114.
- Breder, C.M. Jr, 1967. On the survival value of fish schools. *Zoologica*, **52**, 25-40.
- Breder, C.M. Jr, 1976. Fish schools as operational structures. *Fishery Bulletin, National Oceanic and Atmospheric Administration, Washington DC*, **74**, 471-502.
- Brock, V.E. & Riffenburgh, R.H., 1960. Fish schooling: a possible factor in reducing predation. *Journal du Conseil Permanent International pour l'Exploration de la Mer*, **25**, 307-317.
- Cone, C.D. Jr, 1962. Thermal soaring of birds. *American Scientist*, **50**, 180-209.
- Daws, R.W., Williams, T.M. & Kooyman, G.L., 1985. Swimming metabolism of yearling and adult harbor seals *Phoca vitulina*. *Physiological Zoology*, **58**, 590-596.
- Dyer, A.B. & Gottlieb, C., 1990. Auditory basis of maternal attachment in ducklings (*Anas platyrhynchos*) under simulated naturalistic imprinting conditions. *Journal of Comparative Psychology*, **104**, 190-194.
- Fancy, S.C. & White, R.G., 1985. Incremental cost of activity. In *Bioenergetics of wild herbivores* (ed. R.J. Hudson and R.G. White), pp. 143-159. Boca Raton, Florida: CRC Press.
- Fields, P.A., 1990. Decreased swimming effort in groups of Pacific mackerel (*Scomber japonicus*). *American Zoologist*, **30**, 134A.
- Fish, F.E., 1982. Aerobic energetics of surface swimming in the muskrat *Ondatra zibethicus*. *Physiological Zoology*, **55**, 180-189.
- Fish, F.E., 1984. Mechanics, power output and efficiency of the swimming muskrat (*Ondatra zibethicus*). *Journal of Experimental Biology*, **110**, 183-201.
- Fish, F.E., 1992. Aquatic locomotion. In *Mammalian energetics: interdisciplinary views of metabolism and reproduction* (ed. T.E. Tomasi and T.H. Horton), pp. 34-63. Ithaca, New York: Cornell University Press.
- Fish, F.E., Fegely, J.F. & Xanthopoulos, C.J., 1991. Burst-and-coast swimming in schooling fish with implications for energy economy. *Comparative Biochemistry and Physiology*, **100A**, 633-637.
- Gross, A.C., Kyle, C.R. & Malewicki, D.J., 1983. The aerodynamics of human-powered land vehicles. *Scientific American*, **249** (6), 126-134.
- Hainsworth, F.R., 1987. Precision and dynamics of positioning by Canada geese flying in formation. *Journal of Experimental Biology*, **128**, 445-462.
- Hertel, H., 1966. *Structure - form - movement*. New York: Rheinhold.
- Hess, E.H., 1959. Imprinting. *Science, New York*, **100**, 133-141.
- Higdon, J.J.L. & Corsin, S., 1978. Induced drag of a bird flock. *American Naturalist*, **112**, 727-744.
- Hill, R.W., 1972. Determination of oxygen consumption by use of paramagnetic oxygen analyzer. *Journal of Applied Physiology*, **33**, 261-263.
- Hoerner, S.F., 1965. *Fluid-dynamic drag*. Midland Park, New Jersey: Hoerner.

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- Hoyt, D.F. & Taylor, C.R., 1981. Gait and the energetics of locomotion in horses. *Nature, London*, 292, 239-240.
- Hummel, D., 1983. Aerodynamic aspects of formation flight in birds. *Journal of Theoretical Biology*, 104, 321-347.
- Kyle, C.R., 1979. Reduction of wind resistance and power output of racing cyclists and runners traveling in groups. *Ergonomics*, 22, 387-397.
- Lissaman, P.B.S. & Shollenberger, C.A., 1970. Formation flight of birds. *Science, New York*, 168, 1003-1005.
- Noms, K.S. & Prescott, J.H., 1961. Observations on Pacific cetaceans of Californian and Mexican waters. *University of California Publications in Zoology*, 63, 291-402.
- Orthmeyer, D.L. & Ball, I.J., 1990. Survival of mallard broods on Benton Lake National Wildlife Refuge in northcentral Montana. *Journal of Wildlife Management*, 54, 62-66.
- Partridge, B.L. & Pitcher, T.J., 1979. Evidence against hydrodynamic function for fish schools. *Nature, London*, 279, 418-419.
- Pennycuik, C.J., 1972. Soaring behaviour and performance of some East African birds, observed from a motor-glider. *Ibis*, 141, 178-218.
- Prandtl, L. & Tietjens, O.C., 1934. *Applied hydro and aerodynamics*. New York: Dover.
- Prange, H.D. & Schmidt-Nielsen, K., 1970. The metabolic cost of swimming in ducks. *Journal of Experimental Biology*, 53, 763-777.
- Pugh, L.G.C.E., 1971. The influence of wind resistance in running and walking and the mechanical efficiency of work against horizontal or vertical forces. *Journal of Physiology*, 213, 255-276.
- Rayner, J.M.V., 1985. Vorticity and propulsion mechanics in swimming and flying animals. In *Konstruktionsprinzipien lebender und ausgestorbener Reptilien* (ed. J. Riess and E. Frey), pp. 89-118. Tübingen: University of Tübingen.
- Schmidt-Nielsen, K., 1972. Locomotion: energy cost of swimming, flying and running. *Science, New York*, 177, 222-228.
- Shaw, E., 1978. Schooling fishes. *American Scientist*, 66, 166-175.
- Stephenson, R., Lovvorn, J.R., Heieis, M.R.A., Jones, D.R. & Blake, R.W., 1989. A hydromechanical estimate of the power requirements of diving and surface swimming in lesser scaup (*Aythya affinis*). *Journal of Experimental Biology*, 147, 507-518.
- Tucker, V.A., 1975. The energetic cost of moving about. *American Scientist*, 63, 413-419.
- Vogel, S., 1981. *Life in moving fluids: the physical biology of flow*. Boston: Willard Grant Press.
- Vogel, S. & LaBarbera, M., 1978. Simple flow tanks for research and teaching. *Bioscience*, 28, 638-643.
- Weihls, D., 1972. Semi-infinite vortex trails, and their relation to oscillating airfoils. *Journal of Fluid Mechanics*, 54, 679-690.
- Weihls, D., 1973. Hydromechanics of fish schooling. *Nature, London*, 241, 290-291.
- Weihls, D., 1974. Energetic advantages of burst swimming of fish. *Journal of Theoretical Biology*, 48, 215-229.
- Weihls, D., 1975. Some hydrodynamical aspects of fish schooling. In *Swimming and flying in nature*, vol. 2 (ed. T.Y.T. Wu, C.J. Brokaw and C. Brennen), pp. 703-717. New York: Plenum Press.
- Weihls, D., 1978. Tidal stream transport as an efficient method for migration. *Journal du Conseil Permanent International pour l'Exploration de la Mer*, 38, 92-99.
- Weihls, D. & Webb, P.W., 1983. Optimization of locomotion. In *Fish biomechanics* (ed. P.W. Webb and D. Weihls), pp. 339-375. New York: Praeger.
- Williams, T.M., 1983. Locomotion in the North American mink, a semi aquatic mammal. I. Swimming energetics and body drag. *Journal of Experimental Biology*, 103, 155-168.
- Williams, T.M., 1989. Swimming by sea otters: adaptations for low energetic cost locomotion. *Journal of Comparative Physiology*, 164A, 815-824.
- Williams, T.M., Friedl, W.A., Fong, M.L., Yamada, R.M., Sedivy, P. & Haun, J.E., 1992. Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. *Nature, London*, 355, 821-823.
- Woakes, A.I. & Butler, P.J., 1983. Swimming and diving in tufted ducks, *Aythya fuligula*, with particular reference to heart rate and gas exchange. *Journal of Experimental Biology*, 107, 311-329.