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Kinematics of Ducklings Swimming in Formation: Consequences of Position

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ABSTRACT The kinematics of the paddling stroke of ducklings swimming in formation were analyzed to detect differences in relation to swimming effort and position in the formation. Paddling motions of the feet were filmed as ducklings swam in a constant 0.3 m/s water current behind a decoy which could be in the water or suspended above the water. Ducklings were tested in clutches of one, two, and four ducklings at ages of **3, 7,** and **14** days of age. Ducklings swam in organized formations with the lead duckling 0.25 body length posterior of the decoy and with an average interduckling distance of 0.1 body length. Stroke frequency was constant within any age and decreased with age. Age, decoy position, and clutch size affected the length of the arc traversed by the foot through the power stroke for the most posterior duckling in the formation. Trailing ducklings had an arc length 16.9% less than leading ducklings, and ducklings swimming in formation had an arc length as much as 29.8% less than a solitary duckling. These results suggest that mechanical energy is conserved when formation swimming is employed. © 1995 Wiley-Liss, Inc.

Many animals travel in highly organized formations. This behavior has been hypothesized to reduce energy expenditure and enhance locomotor performance of individuals. Although applied to all modes of locomotion including walking (Fancy and White, '85), saving energy by moving in formation is considered most practical in swimming (Breder, '76; Weihs, '73) and flying (Hummel, '83; Lissaman and Schollenberger, '70). 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" for a reduction in drag (Hagberg and McCole, '90; Kyle, '79; Romberg et al., '71).

Energy savings have been difficult to measure for animal locomotion. The three-dimensional complexity, uncontrolled and inconsistent positioning of individuals in the formation, and large size of polarized animal formations, such as fish schools and V formations of geese, have deterred experimentation to evaluate hypotheses of energy savings by formation movement (Breder, '76; Hummel, '83; Shaw, '78). Previous analyses of energy savings by formation movement in animals focused on aero- and hydrodynamic models (Badgerow and Hainsworth, '81; Cutts and Speakman, '94; Higdon and Corrsin, '78; Hummel, '83; Kshatriya and Blake, '92; Lissaman and Schollenberger, '70; Weihs, '73, '75). These models predict significant energy savings when animals are arranged in appropriate formations. Observations on bird flocks and fish schools indicate, however, that individuals often deviate from the optimal configuration (Badgerow and Hainsworth, '81; Cutts and Speakman, '94; Fish et al., '91; Hainsworth, '87; Partridge and Pitcher, '79).

Kinematics and drag on animals in water have been used as indirect measurements to test the presumption of energy economy by formation swimming. Fish in schools swam two to six times longer than single fish (Belyayev and Zuyev, '68), increasing coast times during burst-and-coast swimming (Fish et al., '91) and reducing tail-beat frequency (Fields, '90). Queues of spiny lobsters *(Panulirus argus)* in water were shown to sustain less drag per individual than a single lobster traveling at the same speed (Bill and Herrnkind, '76). The reduction in energetic cost per individual in a queue was a direct function of queue length.

The following behavior by ducklings is regarded as being advantageous through increased growth

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rates, decreased predation, increased thermoregulatory control, and increased locomotor effectiveness (Bellrose, '76; Fish, '94; Shaw, '78). The metabolic energy savings of formation swimming by mallard ducklings (*Anas platyrhynchos)* following a decoy was examined by Fish ('94). Mallard ducklings were well suited for metabolic examination of formation swimming owing to their habit of swimming in single file. The single-file formation reduced the complexity of the water flow and its interaction with individual animals. The metabolic rate per individual decreased with increasing clutch size by 7.8–43.5% (Fish, '94). Maximum individual energy savings of 63% was realized by four 3-day-old ducklings swimming in the decoy's wake compared to a solitary duckling.

The purpose of this study is to determine what effect position within a formation has in regard to locomotor effort of ducklings. By examining the kinematics of swimming motions, an indirect measure of an individual's energy use can be determined with regard to an exact position within the formation. Kinematic data were collected simultaneously with the metabolic data previously reported (Fish, '94).

MATERIALS AND METHODS

Experimental animals

One-day-old mallard ducklings *(Anus platyrhynchos)* were obtained commercially. Ducklings were imprinted individually to a female mallard duck decoy Ducklings display a following response that is imprinting (Bolhuis, '91; Dyer and Gottlieb, '90; Hess, '59) and are capable of being led to water within the first 12 hr after hatching (Bellrose, '76). Initial imprinting was accomplished by towing the decoy around a circular arena (1.2 m diameter) for a 5- to 10-min period. The majority of ducklings continuously followed the decoy within 2 min. After initial imprinting, ducklings were assigned into three experimental clutches of one, two, and four ducklings. Clutches were trained daily to swim for 20–30 min at 0.3 ms^{-1} behind the decoy in a recirculating water channnel (see *Water channel).*

Clutches were caged separately Ducklings were maintained on a light cycle of 12L:12D at ambient temperatures of 20–25°C. An infrared heat lamp was provided during the 1st week. A diet of starter duck feed and water were supplied ad libitum.

Water channel

Experiments and swim training were conducted in a recirculating water channel (Fig. 1) based on designs of Vogel and LaBarbera ('78). The water channel was constructed of clear Lucite. Ducklings were tested in the working section (1.2 x 0.6 x 0.44 m) of the channel. The upstream end of the working section was bounded by a plastic grid (commercially termed "egg crate") to reduce turbulence in the flow. The downstream end of the working section was bounded by wire mesh. Water velocity (U, ms^{-1}) was controlled by two electric outboard motors (Minn Kota 65MX) located in the return channel. Power to the motors was provided by two 12-V storage batteries. The relationship between motor speed and water speed was determined with a Marsh-McBirney portable flowmeter (model 201). Because ducklings swimming against the water current remained stationary relative to their position in the water channel, water velocity and swimming speed were equivalent.

A Lucite metabolic chamber was fitted over the working section of the water channel (Fig. 1). The chamber provided a large enough space to allow ducklings to organize into formations and avoided interference with flow and wave patterns generated by the animals. **A** hole in the top of the chamber allowed a threaded bolt fitted to the decoy to pass through. The decoy could be raised above the water surface or lowered into the flowing water. The decoy had a waterline length of 0.30 m and a maximum width of 0.16 m. Air was drawn through the chamber and metabolic rate was measured from open circuit respirometry (Fish, '94).

Kinematic analysis

The position of the ducklings in formation and with respect to the decoy was monitored with a video camera (Panasonic Camcorder PV-510). To videotape a dorsal view of the ducklings in the water channel, a mirror was suspended at a 45" angle above the working section. Illumination was provided by a bank of four 500-W flood lamps suspended above the water channel.

To determine the kinematics of the paddling stroke, the lateral view of the feet of swimming ducklings was filmed with either cine or video cameras. Ciné films were made at 64 frames s^{-1} with a Bolex H-16 ciné camera equipped with a Kern Vario-Switar 100 POE zoom lens (1:1.9, f 16–100 mm) using 16-mm film (Kodak 4-X reversal film 7277, ASA 400). Film records were analyzed by sequentially projecting individual frames of film with a stop-action projector (Lafeyette Instrument Co., model 00100). Projections were measured with a digitizer tablet (GTCO, Digi-Pad 21A71D4) interfaced to an IBM PC microcomputer.

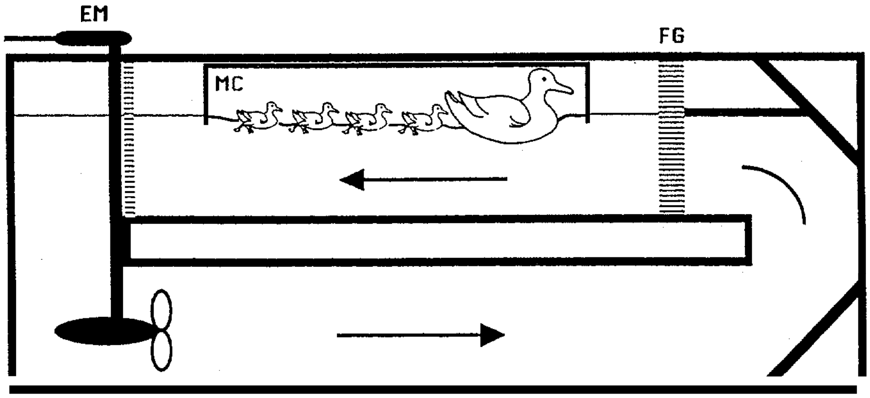

Fig. 1. Diagram showing lateral view of the recirculating flow channel that was used to measure spacing and kinematics of ducklings swimming in formation. Water velocity was controlled by two electric motors (EM). Flow direction is indicated by the arrows in the working section and return sections of the channel. Flow was straightened as it passed into the working section through a plastic flow grid (FG). Ducklings and the decoy were confined to a metabolic chamber (MC). Mean water temperature was 21.6° with a standard deviation of ±1.0°.

Video images of paddling feet were recorded at 60 Hz with Panasonic Video Cassette Recorder **AG-7300** and Panasonic System Camera (WV-D5100) equipped with a Panasonic (WV-LZ14/12) 12X zoom lens (1:1.6, f 10.5-126 mm). **A** time-code signal was recorded on the videotape with Horita TRG-50 SMPTE time-code generator. Sequential foot positions were digitized from individual fields of videotape with Peak Performance Technologies video analysis system (Peak 2D, Version 4.2.4).

Data were acquired only from records in which ducklings swam steadily with no apparent motion of the body relative to the camera. Spacing between the centerpoints of the decoy and the first duckling and between ducklings were measured from videotape of the dorsal view. Data were collected over a 5-min period of steady swimming at 1-min intervals to compute an average distance between centerpoints.

The kinematic variables included stroke frequency (*f,* Hz), time of power phase of stroke cycle (*tp,* s), time of recovery phase of stroke cycle (*tr;* s), start angle (As, deg; angle between longitudinal axis of foot and horizontal at start of power phase), finish angle (*Af,* deg; angle between longitudinal axis of foot and horizontal at end of power phase), arc angle (*Aa,* deg; difference between ***Af*** and As), and arc length (*Al,* m; distance traversed through power phase of distal-most point of foot).

Experimental procedure and statistical analysis

Twelve groups of three clutches (one, two, and four ducklings) were examined. Each experimental clutch was tested at **3, 7,** and 14 days of age. The Reynolds numbers for **3-,** 7-, and 14-day-old ducklings and for the decoy were 2.15×10^4, 2.82×10^4, 3.60×10^4, and 8.94×10^4, respectively, based on waterline length (Fish, '94; Vogel, '81). 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-day period, each clutch was tested with the decoy in the up (raised) or down (lowered) position. Order of testing was assigned randomly Kinematic data were collected on all ducklings swimming in formation in clutches of one and two ducklings, but data were collected only on the first and last ducklings in a clutch of four.

Data were analyzed using a three-factor analysis of variance (ANOVA; DataDesk and Statistical with repeated measures. Kinematic variables were analyzed separately for leading and trailing ducklings in the formation, because in a clutch of one the solitary animal represented both the leading and trailing duckling. Differences between levels of factors were examined using paired t-test procedures. Variation about means is expressed as ± 1 standard error (SE).

RESULTS

Formation configuration

Mean masses for 3-day, 7-day, and 14-day-old ducklings over the test period were 0.054 ± 0.001

kg, 0.109 ± 0.001 kg, and 0.243 ± 0.004 kg, respectively

Ducklings readily followed the decoy when swimming in the water channel (Fig. 2). Distances between centerpoints of ducklings are provided in Table 1. Solitary or leading ducklings maintained an average position of 0.30, 0.16, and 0.28 body lengths posterior of the decoy for 3-, 7-, and 14-day-old ducklings, respectively. ANOVA showed significant effects on distance between the decoy and first duckling with respect to age ($P < .001$) and position of the decoy in the water ($P < .023$). The distance between the decoy and first duckling was greater with the decoy producing a wake (Table 1). 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. Using ANOVA, significant effects for four duckling formations were found for duckling age ($P < .001$), decoy position ($P < .001$), and position of the duckling within the formation ($P < .035$). Inter-duckling distances for 3- and 7-day-old ducklings were small and averaged less than 1% of body length. Distances between 14-day-old ducklings averaged 26% of body length. The largest distance was between the third and fourth duckling; the shortest distance was between the second and third duckling in the formation (Table 1). The latter distance was primarily due to the tendency of the middle two ducklings to swim abreast producing the diamond formation. Ducklings would reposition themselves frequently throughout the testing period by exchanging position with another duckling in the formation.

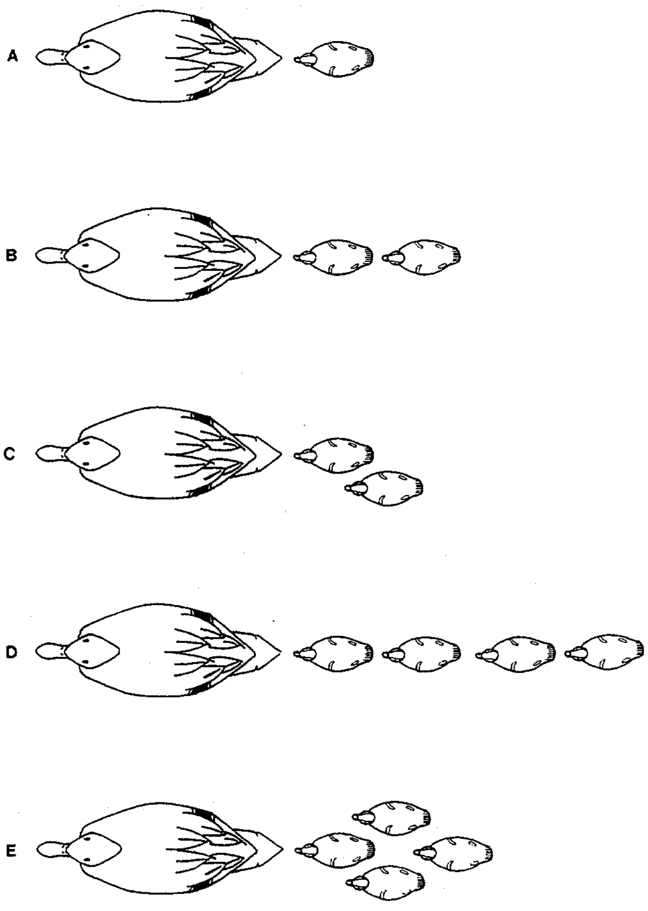

Fig. 2. Typical duckling formations for clutches of one, two, and four individuals. Single-file formations are shown in **A**,**B**,**D**; echelon formation is shown in **C**: diamond formation is shown in E (after Fish, '94).

The various formation patterns employed by the ducklings swimming in a clutch of four made it difficult to distinguish the feet of individual animals. This was apparent particularly when ducklings swam abreast. Therefore analysis of foot motion was confined to the lead duckling and to the trailing-most duckling in the clutch. No bias was assumed for individual ducklings, because position between individuals changed throughout an experimental trial.

Kinematic variables

All ducklings swam using alternate paddling of the feet. The paddling motion was composed of power and recovery phases. During the power phase the foot was swept posteriorly through an arc with the interdigital webbing fully spread. During the recovery phase the foot was swept anteriorly To reduce drag during recovery by a reduction of foot area (Fish, '84), the webbing of the foot was collapsed by adduction and plantarflexion of the digits.

A summary of the results from ANOVA for leading and trailing ducklings is displayed in Table 2. The age factor significantly ($P < .05$) affected all kinematic variables with the exception of As. Decoy position affected only Al ($P < .005$). For leading ducklings, significant differences between clutch size ($P < .01$) were found only for the time of the power phase, whereas for trailing ducklings, clutch size affected tp, As, Aa, and Al.

Frequency remained constant within each of the different age classes with pooled means of **4.55** ± 0.06 Hz, 4.29 ± 0.05 Hz, and 3.71 ± 0.07 Hz for ages of 3, 7, and 14 days, respectively The paddling frequency decreased significantly with in-

*TABLE 1. Distances (mean ± SE) between centerpoints of ducklings and decoy in formation**

		Age (days)					
		3		7		14	
Clutch size	Distance	U	D	U	D	U	D
1	D-1	0.22 ± 0.03	0.21 ± 0.01	0.21 ± 0.01	0.22 ± 0.01	0.22 ± 0.01	0.27 ± 0.01
2	D-1	0.20 ± 0.02	0.20 ± 0.01	0.20 ± 0.01	0.22 ± 0.01	0.22 ± 0.01	0.27 ± 0.03
4	D-1	0.20 ± 0.02	0.22 ± 0.00	0.20 ± 0.01	0.22 ± 0.01	0.23 ± 0.01	0.25 ± 0.01
2	1–2	0.08 ± 0.00	0.07 ± 0.00	0.08 ± 0.00	0.07 ± 0.00	0.16 ± 0.01	0.15 ± 0.01
4	1–2	0.07 ± 0.01	0.08 ± 0.01	0.11 ± 0.00	0.09 ± 0.00	0.13 ± 0.01	0.13 ± 0.01
4	2–3	0.06 ± 0.00	0.06 ± 0.01	0.10 ± 0.01	0.09 ± 0.01	0.14 ± 0.01	0.14 ± 0.01
4	3–4	0.08 ± 0.01	0.08 ± 0.01	0.12 ± 0.01	0.11 ± 0.01	0.20 ± 0.01	0.16 ± 0.01

*Position of the decoy above the water and in the water is indicated by U and D, respectively. Distances are provided as the intervals between centerpoints of the decoy (D) and ducklings in order of position (1–4).

creasing age from 3 to 7 days ($P < .005$) and from 7 to 14 days ($P < .001$). The time of the power phase, *tp,* was shorter in duration than *tr* for all ages ($P < .001$). Both *tp* and *tr* increased with increasing age (Fig. 3). As a consequence, *tp* remained a constant fraction (approximately 47%) of the duration of the entire paddling cycle for ducklings of all different sizes.

The angular changes of foot position throughout the power phase are shown in Figure 4. As showed no significant differences between age groups. The pooled mean for As was 33.79 ± 0.81" (n = 316). For *Af,* no significant difference was found between 3- and 7-day-old ducklings; however, a significant decrease ($P < .012$) occurred as age increased to 14 days. Similarly, Aa remained relatively constant for 3- and 7-day-old ducklings at 85.37 ± 1.94" and 85.71 ± 1.66°, respectively, and decreased to 79.88 ± 1.59° at 14 days (Fig. 4).

The only variable to consistently and significantly be affected ($P < .005$) by all factors was AI (Table 2). *Al* was used therefore to test differences between leading and trailing ducklings in formation. The single duckling with the decoy in the up position was used as a reference for comparison of *Al* for effects due to the decoy position and increasing clutch size. Results for leading and trailing ducklings are illustrated in Figures 5 and 6. **As** with other kinematic variables, *Al* was affected generally by age, showing a positive relationship with increasing age.

With the decoy in the up position, lead ducklings showed a 3.8–16.7% reduction in *Al* with increasing clutch size (Fig. 5). Only the lead 3-day-old duckling in a clutch of two had a significant reduction ($P < .05$) of *Al* compared to a solitary duckling. In comparison to leading ducklings, trailing ducklings had greater reductions in *Al* by 7.5–23.3% with increasing clutch size (Fig. 5). This effect was greatest for 3- and 7-day ducklings. Significant effects were noted for trailing ducklings in a clutch of two at 3 days ($P < .05$) and in a clutch of four at 7 days of age ($P < .01$). Significant differences between lead and trailing ducklings were found for 7 day olds in clutches of two ($P < .03$) and four ($P < .003$).

The effect of the wake of the decoy was evident from the results of *Al* for both leading and trailing ducklings (Fig. 6). Comparison of solitary ducklings showed a 16.7–4.7% reduction of *Al* due to the effect of the decoy The maximum 16.7%

TABLE 2. Results from ANOVA of kinematic variables for leading and trailing ducklings"

	Duckling position					
	Lead			Trail		
Variable	Clutch size	Decoy	Age	Clutch size	Decoy	Age
Frequency	– – –	– – –	+++	– – –	– – –	+++
Power time	++	– – –	+++	+++	– – –	+++
Recovery time	– – –	– – –	+++	– – –	– – –	+++
Start angle	– – –	– – –	– – –	+	– – –	– – –
Finish angle	– – –	– – –	– – –	– – –	– – –	+++
Arc angle	– – –	– – –	+	+++	– – –	+++
Arc length	– – –	+++	+++	+++	+++	+++

*(+) $P < .05$; (++) $P < .01$; (+++) $P < .005$.

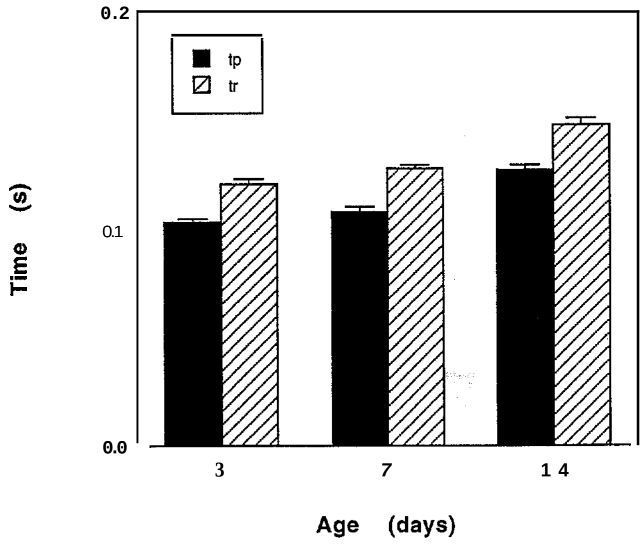

Fig. 3. Results of tp and tr are shown for each age class. Values are pooled from clutch size, decoy position, and position of the duckling within the formation. The error bars indicate 1 standard error.

reduction in Al occurred for individual 7-day-old ducklings and was significant at $P < .05$. With the decoy in the down position, leading ducklings in 3- and 7-day-old clutches and trailing ducklings in all age classes demonstrated significant differences with a solitary duckling at equivalent ages.

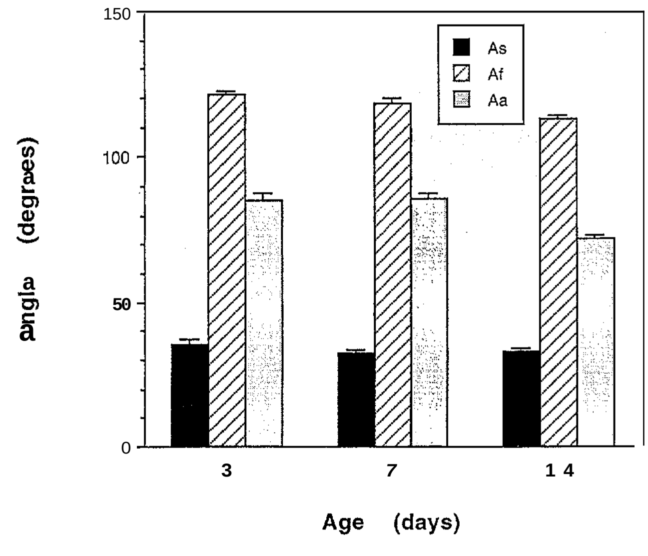

Fig. 4. Angles measured from sweep of paddling feet of ducklings. The **insert** indicates As, Af, and Aa for each age class. Results are pooled from clutch size, decoy position, and position of the duckling within the formation. The error bars indicate 1 standard error.

Three-day-old lead ducklings had a reduction in Al of 22.6% when in a clutch of two. The youngest trailing ducklings showed the greatest reduction of Al (29.8%) due to increasing clutch size. Older ducklings displayed nearly equivalent maximum decreases of Al (16–16.7%) owing to decoy position and clutch size. However, 7-day ducklings did not show a stepped decrease with increasing clutch size. Significant differences between lead and trailing ducklings in the same clutch were found for 3 day olds in a clutch of four ($P < .03$) and for 14 day olds in clutches of two ($P < .03$) and four ($P < .02$).

DISCUSSION

Kinematics

An animal's swimming velocity and mechanical effort are related to the frequency and amplitude of the stroke cycle (Arellano et al., '94; Baudinette and Gill, '85; Webb, '75). Indeed, there is a strong association between energy expenditure and the frequency of locomotor movements (Casey, '92). However, many paddling animals, including mallard ducks, maintain a constant frequency while amplitude varies with swimming velocity (Clark and Fish, '94; Fish, '84, '93; Prange and Schmidt-Nielsen, '70; Williams, '83). The associated changes in amplitude with velocity and effort are indicated by angular displacement or arc traversed by the paddle through the power stroke (Blake, '79; Fish, '84).

The relationship between effort and paddling kinematics was evident for ducklings swimming in formation. Time variables (i.e., f, tp, tr) were not expected to change in accordance with changes in the relative velocity induced by the formation. Indeed, the time variables remained constant and were affected only by the age of the ducklings. The decrease of f with increasing age and body size was consistent with results reported by Clark and Fish ('94) for ducklings swimming individually Although tp and tr also decreased with increasing age, the ratio of tp/tr remained constant at 0.47. Short tp allows for a large thrust force over the power phase, whereas longer tr aids in minimizing drag during recovery (Fish, '84).

Angular variables As, Af, and Aa were not a reliable indicator of velocity changes. A correlation was shown between Aa and swimming speed for surface paddling muskrats in a previous study by Fish ('84). However, in the study on muskrat swimming, the notable change of

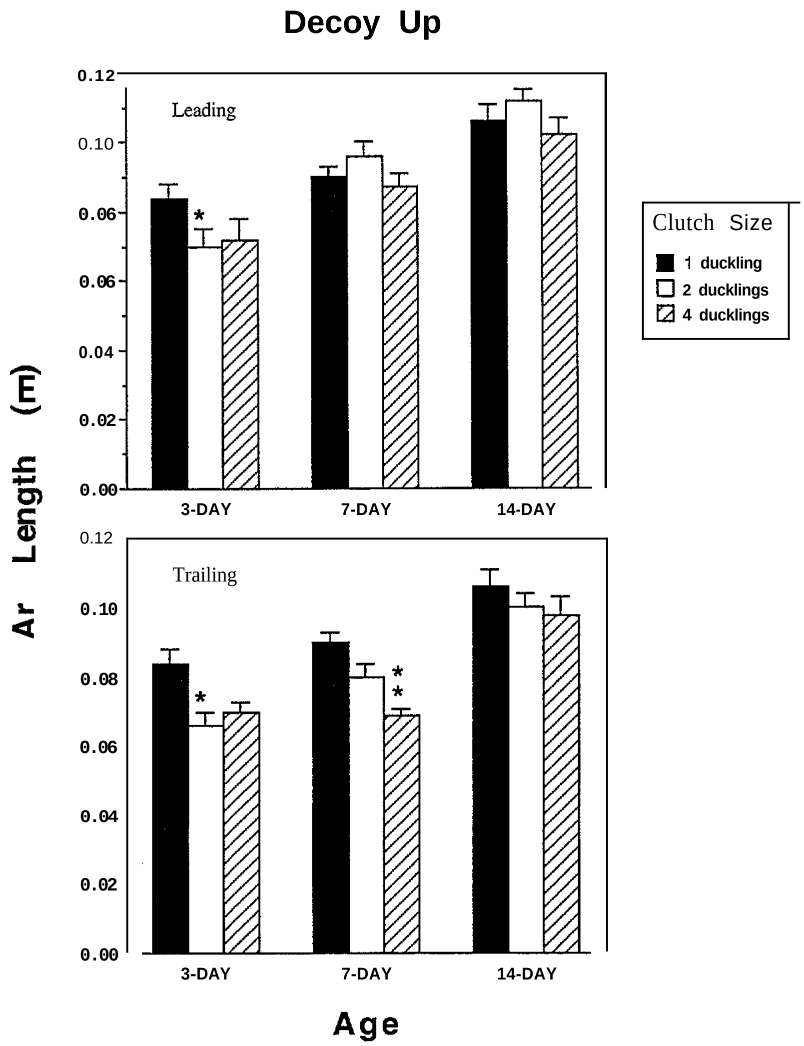

Fig. 5. Comparison of Al between different clutch sizes for leading and trailing ducklings with the decoy out of the water. Reduction in Al indicates a reduced relative velocity and swimming effort. Trailing ducklings exhibited a more pronounced reduction than leading ducklings. The error bars indicate 1 standard error. Asterisks indicate significant differences ($*P < .05$; $**P < .01$) with a solitary duckling swimming behind a decoy in the up position (solid bar).

Aa may have been in part a reflection of the large range in velocity over which measurements were made. In the present study, angular measurements may not have been sensitive enough to detect the smaller changes in the velocity field encountered by the ducklings swimming in formation. In addition, the multiple joints in the duckling leg would permit a wide range of motion without notable change in the angular displacement by the foot. Paddlers with multi-segmental limbs exhibit considerable rotation about the knee while the foot is maintained nearly perpendicular to the direction of motion through a major portion of the power phase (Fish, '84; Gruner and Altman, '80; Johnson and Bekoff, '92). This motion effectively translates the foot to increase thrust production.

Changes in swimming effort owing to the formation size and position within the formation were indicated by the displacement variable AZ. Paddling is a drag-based propulsion whereby drag on the foot is used to generate forward thrust for the body (Alexander, '83; Fish, '93). The foot drag is dependent directly on the backward velocity of the foot relative to the water during the power phase (Alexander, '83). For the same tp and swimming velocity, a foot with a shorter Al has a lower foot velocity than with a

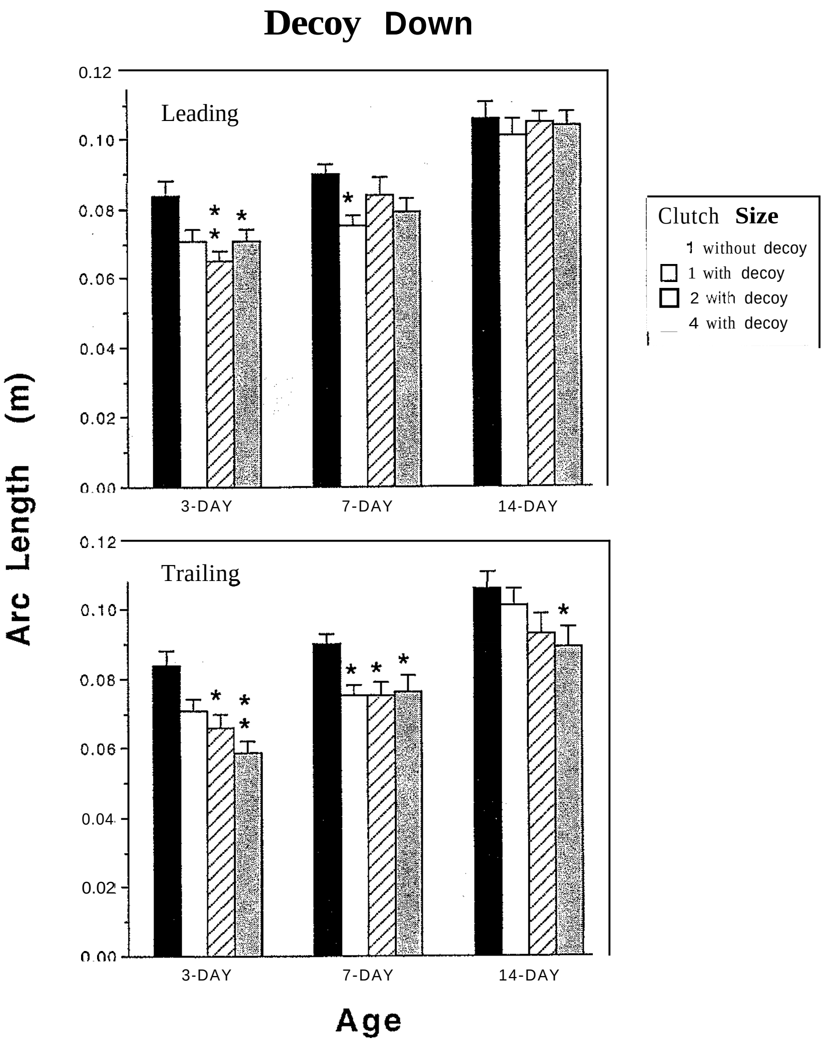

Fig. 6. Comparison of *Al* between different clutch sizes for leading and trailing ducklings with the decoy in the water. The solid bar is the same as in Figure 5 for a solitary duckling swimming behind a decoy in the up position. Asterisks indicate significant differences ($*P < .05$; $**P < .01$) between ducklings swimming in the wake of the decoy and a solitary duckling (solid bar). The error bars indicate 1 standard error.

longer *Al*. Thus the duckling with a shorter *Al* produces less thrust and requires less energy. Ducklings following in the wake of the decoy had lower *Al* compared to ducklings without the decoy's wake, regardless of position in the formation. The decrease in *Al* declined with age, so that 3-day-old ducklings benefited the most from swimming behind the decoy. In addition, *Al* declined with increasing clutch size indicating an advantage to larger formations.

The kinematics described in this study were collected simultaneously with metabolic data already reported by Fish ('94). The trends observed for the kinematics were similar with those trends recorded for the active metabolic rates of the ducklings. Metabolic rates per duckling decreased with increasing clutch size and with the influence of the wake of the decoy. In addition, as age increased, energy savings due to formation swimming decreased. Although the kinematics of duckling swimming provides an adequate indication of swimming effort, the magnitude of the reduction in effort reflected by the kinematics was smaller than for metabolic rates (Fish, '94). Variations in the degree of response may reflect differences in collecting kinematic versus metabolic data. Metabolic measurements were made over the entire swimming trial (Fish, '94), whereas kinematic data were obtained from relatively short durations.

Positional effects

The results of this study indicate that the least energetic effort is expended by the most posterior duckling in formation. Compared to a solitary duckling, trailing ducklings had values of *Al* that were 3.4–20.0% lower than leading ducklings with and without the decoy's wake. This finding suggests that the trailing duckling swims in a flow field different from the more anterior ducklings.

The flow field for the trailing duckling is produced from the vortex street shed from more anterior animals (Fish, '94; Hoerner, '65; Prandtl and Tietjens, '34; Vogel, '81). The vortex street consists of a wake of alternating vortices which are regularly arranged as two staggered rows (Hoerner, '65; Prandtl and Tietjens, '34; Vogel, '81). Vorticity transports momentum within the fluid and affects the velocity profile. Changes in the velocity profile of the fluid influence the relative velocity of trailing bodies in the wake (Belyayev and Zuyev, '68; Breder, '65, '76; Weihs, '73, '75). Relative velocity is calculated as the difference between a trailing body's velocity and the mean velocity induced by the vortices shed from a leading body (Weihs, '73). A trailing body experiences a reduction of its relative velocity when oriented in the same direction as the mean velocity of the vorticity A decrease in the relative velocity can decrease drag, which is directly proportional to the velocity squared. Lowered drag requires reduced energy to generate thrust, which is equal to the drag for steady swimming. When drag was measured on two circular cylinders, one placed behind the other, the drag on the trailing cylinder was reduced by approximately 75% (Hoerner, '65). Furthermore, the drag on the second cylinder decreased with a decrease in the spacing ratio (distance between the cylinders divided by the cylinder diameter) below 3 (Hoerner, '65).

For rigid bodies such as those of ducks, the optimal configuration is a single-file formation (Bill and Herrnkind, '76; Fish, '94; Weihs, '73). Vorticity generated by the anterior ducklings provides momentum to the water in the same direction as the ducklings. Momentum transported in the water would be imparted to the trailing duckling which would experience reduced drag and energy expense. This effect would be improved by the low spacing ratio (<0.52) between ducklings. Bill and Herrnkind ('76) found that reduced spacing within a queue of spiny lobsters markedly decreased drag. Furthermore, queues of lobsters have lower drag per individual compared to the solitary animal, and drag reductions are enhanced with greater numbers of individuals in the queue (Bill and Hernnkind, '76).

The most posterior duckling swimming in formation is in the optimal position for drag reduction because the vortex street in the wake narrows (Hoerner, '65; Van Dyke, '82). As the street narrows the strength of the vorticity on trailing bodies increases. The advantage for drag reduction is greatest where the vortex street is narrowest. This point would be reached at about two to four diameters of the decoy (0.32–0.64 m), so that the wake would still be coalescing at the distance of the first ducklings (Weihs, personal communication). Furthermore, the trailing duckling will have an energetic advantage when swimming in a diamond formation. Because momentum is directly proportional to mass, the middle two ducklings swimming abreast would affect a larger mass of water in their wake compared to a single duckling. In this formation, a single trailing duckling would have more momentum transferred to it to be more effectively pulled along. When drafting behind a more massive body such as an automobile, human cyclists realized energy savings of 62% (Hagberg and McCole, '90) and achieved speeds over 220 km hr^{-1} (Gross et al., '83).

In addition to the beneficial flow field produced by the drag wake (vortex street) of the decoy and leading ducklings, the thrust wake produced by the paddling movements of the duckling feet may aid in reducing swimming costs for the trailing duckling. During the power phase of stroke cycle, the foot is swept posteriorly, generating a pair of vortices with one vortex located directly above the other (Alexander, '83). Because of the rotation of thrust-type vortices (Weihs, '72), the body of the trailing duckling should experience a low relative velocity as it encounters the more dorsal vortex. In addition, paddling movements of the feet of the trailing duckling may be able to reposition and use the energy of oncoming vortices from leading ducklings to increase propulsive efficiency (Gopalkrishnan et al., '94). Ducklings are expected to show a greater energetic benefit when swimming in the thrust wake of an actively paddling adult (Fish, '94).

For single-file formations, only studies on human cyclists and motor vehicles have examined the effect of spacing and position on energy economy Kyle ('79) found a greater drag reduction the more closely one cyclist followed another. Drafting cyclists experience a 26–33% energy savings in a pace line (Hagberg and McCole, '90; Kyle, '79), and greater savings are obtained when following in a pack (Hagberg and McCole, '90; Kyle, '79; McCole et al., '90). A race car drafting another reduces its drag by 37% at a separation distance of 1.1 car lengths, but further significant drag reduction does not occur with decreasing separation distance (Romberg et **al.**, '71). Four cars moving in single-file experience drag reduction for spacings less than one car length (Zabat et al., '94). The trailing vehicle of the four-car platoon has the lowest drag with a drag coefficient 0.62 of the non-drafting value. However as spacing decreases to half a car length, the third vehicle's drag is the lowest of cars in formation and is reduced to 0.50 of the non-drafting value (Zabat et al., '94).

Fish ('94) cautioned against thinking that formation movements in ducklings were used solely or even primarily for energy savings. Formation movements by animals are considered to confer a variety of other benefits, including locating food resources, mating efficiency, pooling orientation information, greater tolerance to toxic substances, and protection against predation (Breder, '67, '76; Brock and Riffenburgh, '60; Magurran, '90; Shaw, '78). The gregarious behavior of ducklings was postulated to function mainly for protection from predators analogous to a convoy system (Lack, '47). Although a duckling swimming in the rear position of a formation may expend the least energy, this position seems intuitively to be at a disadvantage with regard to predation (Hamilton, '71). The duckling is farthest from the protection of the mother. Canada goose (*Branta canadensis)* goslings are protected by monogamous parents (Bellrose, '76). As is typical with other monogamous waterfowl, goslings are led by the mother with the father in the rear (Kear, '70). Increased protection in the front and rear of the formation could contribute to the lower mortality of Canada goose goslings compared to mallard ducklings (Bellrose, '76; Geis, '56; Hanson and Eberhardt, '71; Orthmeyer and Ball, '90). Therefore for ducklings, intermediate positions in the formation may be more cost effective in balancing decreased predation risk and decreased swimming effort.

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LITERATURE CITED

Alexander, R.M. (1983) Locomotion of Animals. Blackie, Glasgow.

Arellano, R., P Brown, J. Cappaert, and R.C. Nelson (1994) Analysis of 50-, 100-, and 200-m freestyle swimmers at the 1992 Olympic Games. J. Appl. Biomech., *10:*189–199.

Badgerow, J.P., and F.R. Hainsworth (1981) Energy savings through formation flight? A re-examination of the vee formation. J. Theor. Biol., *93:*41–52.

Baudinette, R.V., and P. Gill (1985) The energetics of 'flying' and 'paddling' in water: locomotion in penguins and ducks. J. Comp. Physiol. [B] *155:*373–380.

Bellrose, F.C. (1976) Ducks, Geese and Swans of North America. Stackpole, Harrisburg, PA.

Belyayev, V.V., and G.V Zuyev (1968) Hydrodynamic hypothesis of school formation in fishes. Prob. Ichthy, *9:*578–584.

Bill, R.G., and W.F. Herrnkind (1976) Drag reduction by formation movement in spiny lobsters. Science, *193:*1146–1148.

Blake, R.W. (1979) The mechanics of labriform locomotion. I. Labriform locomotion in the angelfish (Pterophyllum *eimekei*): an analysis of the power stroke. J. Exp. Biol., *82:*255–271.

Bolhuis, J.J. (1991) Mechanisms of avian imprinting: a review Biol. Rev. Camb. Philos. Soc., *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:*25–44.

Breder, C.M., Jr. (1976) Fish schools as operational structures. Fish. Bull., *74:*471–502.

Brock, RE., and R.H. Riffenburgh (1960) Fish schooling: a possible factor in reducing predation. J. Cons. Int. Explor. Mer., *25:*307–317.

Casey, T.M. (1992) Energetics of locomotion. In: Advances in Comparative Environmental Physiology. R.M. Alexander, ed. Springer-Verlag, Berlin, Vol. 11, pp. 251–275.

Clark, B.D., and F.E. Fish (1994) Scaling of the locomotory apparatus and paddling rhythm in swimming mallard ducklings (Anus platyrhynchos): test of a resonance model. J. Exp. Zool., *270:*245–254.

Cutts, C.J., and J.R. Speakman (1994) Energy savings in formation flight of pink-footed geese. J. Exp. Biol. *189:*251–261.

Dyer, A.B., and G. Gottlieb (1990) Auditory basis of maternal attachment in ducklings (Anus *platyrhynchos*) under simulated naturalistic imprinting conditions. J. Comp. Psychol., *104:*190–194.

Fancy, S.G., and R.G. White (1985) Incremental cost of activity. In: Bioenergetics of Wild Herbivores. R.J. Hudson and R.G. White, eds. CRC Press, Boca Raton, FL, pp. 143–159.

Fields, PA. (1990) Decreased swimming effort in groups of Pacific mackerel (Scomber *japanicus*). Am. Zool., *30:*134A.

Fish, F.E. (1984) Mechanics, power output, and efficiency of the swimming muskrat (*Ondatra zibethicus*). J. Exp. Biol., *110:*183–201.

Fish, F.E. (1993) Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. Aust. J. Zool., *42:*79–101.

Fish, F.E. (1994) Energy conservation by formation swimming: metabolic evidence from ducklings. In: Mechanics and Physiology of Animal Swimming. L. Maddock, Q. Bone, and J.M.V. Rayner, eds. Cambridge University Press, Cambridge, pp. 193–204.

Fish, F.E., J.F. Fegely, and C.J. Xanthopoulos (1991) Burst-and-coast swimming in schooling fish with implications for energy economy. Comp. Biochem. Physiol. A, *100:*633–637.

Geis, M.B. (1956) Productivity of Canada geese in the Flathead Valley, Montana. J. Wildl. Manage., *20:*409–419.

Gopalkrishnan, R., M.S. Triantafyllou, G.S. Triantafyllou, and D. Barrett (1994) Active vorticity control in a shear flow using flapping foil. J. Fluid Mech., *274:*1–21.

Gross, A.C., C.R. Kyle, and D.J. Malewicki (1983) The aerodynamics of human-powered land vehicles. Sci. Am., *249:*142–152.

Gruner, J.A., and J. Altman (1980) Swimming in the rat: analysis of locomotor performance in comparison to stepping. Exp. Brain Res., *40:*374–382.

Hagberg, J.M., and S.D. McCole (1990) The effect of drafting and aerodynamic equipment on energy expenditure during cycling. Cycling Sci., *2:*19–22.

Hainsworth, F.R. (1987) Precision and dynamics of positioning by Canada geese flying in formation. J. Exp. Biol., *128:*445–462.

Hamilton, W.D. (1971) Geometry of the selfish herd. J. Theor. Biol., *31:*295–311.

Hanson, W.C., and L.L. Eberhardt (1971) A Columbia River Canada goose population, 1950–1970. Wildl. Monogr., *28:*6–61.

Hess, E.H. (1959) Imprinting. Science, *130:*133–141.

Higdon, J.J.L., and S. Corrsin (1978) Induced drag of a bird flock. Am. Nat., *112:*727–744.

Hoerner, S.F. (1965) Fluid-Dynamic Drag. Published by author, Midland Park, NJ.

Hummel, D. (1983) Aerodynamic aspects of formation flight in birds. J. Theor. Biol., *104:*321–347.

Johnson, R.M., and A. Bekoff (1992) Constrainted and flexible features of rhythmical hindlimb movements in chicks: kinematic profiles of walking, swimming and airstepping. J. Exp. Biol., *171:*43–66.

Kear, J. (1970) The adaptive radiation of parental care in waterfowl. In: Social Behaviour in Birds and Mammals. J.H. Crook, ed. Academic Press, London, pp. 357–392.

Kshatriya, M., and R.W. Blake (1992) Theoretical model of the optimum flock size of birds flying in formation. J. Theor. Biol., *157:*135–174.

Kyle, C.R. (1979) Reduction of wind resistance and power output of racing cyclists and runners traveling in groups. Ergonomics, *22:*387–397.

Lack, D. (1947) The significance of clutch size. Ibis, 89: 302–352.

Lissaman, P.B.S., and C.A. Schollenberger (1970) Formation flight of birds. Science, *168:*103–105.

Magurran, A.E. (1990) The adaptive significance of schooling as an anti-predator defence in fish. Ann. Zool. Fennici, *27:*51–66.

McCole, S.D., K. Claney, J.-C. Conte, R. Anderson, and J.M. Hagberg (1990) Energy expenditure during bicycling. J. Appl. Physiol., *68:*748–753.

Orthmeyer, D.L., and I.J. Ball (1990) Survival of mallard broods on Benton Lake National Wildlife Refuge in north-central Montana. J. Wild. Manage., *54:*62–66.

Partridge, B.L., and T.J. Pitcher (1979) Evidence against a hydrodynamic function for fish schools. Nature, 279: 418–419.

Prandtl, L., and O.G. Tietjens (1934) Applied Hydro- and Aerodynamics. Dover, New York.

Prange, H.D., and K. Schmidt-Nielsen (1970) The metabolic cost of swimming in ducks. J. Exp. Biol., *53:*763–777.

Romberg, G.F., F. Chianese, Jr., and R.G. Lajoie (1971) Aerodynamics of race cars in drafting and passing situations. Soc. Auto. Eng. Paper 710213.

Shaw, E. (1978) Schooling fishes. Am. Sci., *66:*166–175.

Van Dyke, M. (1982) An Album of Fluid Motion. The Parabolic Press, Stanford, CA.

Vogel, S. (1981) Life in Moving Fluids. Willard Grant Press, Boston.

Vogel, S., and M. LaBarbera (1978) Simple flow tanks for research and teaching. Bioscience, *28:*638–643.

Webb, P.W. (1975) Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Bd. Can., *190:*1–158.

Weihs, D. (1972) Semi-infinite vortex trails, and their relation to oscillating airfoils. J. Fluid Mech., *54:*679–690.

Weihs, D. (1973) Hydromechanics of fish schooling. Nature, 241:290–291.

Weihs, D. (1975) Some hydrodynamical aspects of fish schooling. In: Swimming and Flying in Nature. T.Y. Wu, C.J. Brokaw, and C. Brennen, eds. Plenum Press, New York, Vol. 2, pp. 703–718.

Williams, T.M. (1983) Locomotion in the North American mink, a semi. I. Swimming energetics and body drag. J. Exp. Biol., *103:*155–168.

Zabat, M., S. Frascaroli, and F.K. Browand (1994) Drag measurements on 2, 3 and 4 car platoons. Soc. Auto. Eng. Paper 940421.