Aquatic turning performance by the whirligig beetle: constraints on maneuverability by a rigid biological system

Frank E. Fish[1],* and Anthony J. Nicastro[2]

[1]*Department of Biology* and [2]*Department of Physics, West Chester University, West Chester, PA 19383, USA*

*Author for correspondence (e-mail: ffish@wcupa.edu)

Summary

Turning performance is constrained by morphology, where the flexibility of the body and the mobility and position of the control surfaces determine the level of performance. The use of paddling appendages in conjunction with the rigid bodies of aquatic arthropods could potentially limit their turning performance. Whirligig beetles (Coleoptera: Gyrinidae) are rigid-bodied, but these aquatic insects can swim rapidly in circular patterns. Turning performance of swimming whirligig beetles (*Dineutes horni*) was assessed by videotaping beetles in a small (115 mm diameter) arena at 500 frames s^{-1} and 1000 frames s^{-1}. Curved trajectories were executed as continuous powered turns. Asymmetrical paddling of the outboard legs was used to power the turn. Turns were produced also by abduction of the inboard elytra and vectored thrust generated from sculling of the wing at 47.14 Hz. The abducted elytra increased drag and acted as a pivot. Swimming speeds varied from 0.06 m s^{-1} to 0.55 m s^{-1} (4.7–44.5 L s^{-1}). Relative minimum radius was 24% of body length. Maximum rate of turn was 4428 degrees s^{-1} with maximum centripetal acceleration of 2.86 g. Turning radius was weakly associated with swimming velocity, although minimum values of the radius showed no correlation with velocity. Turning rate was also related indirectly to radius and directly to centripetal acceleration. Compared to vertebrates with flexible bodies, the relative turning radius of whirligig beetles is constrained by a rigid body and use of drag-based propulsive mechanisms. However, these mechanisms permit continuous turning, and the size of the beetle permits higher turn rates with lower centripetal accelerations.

Introduction

Various morphologies that foster maneuverability have evolved within aquatic animal lineages (Webb, 1984, 1997; Weihs, 1993; Webb et al., 1996; Gerstner, 1999; Fish, 2002). Turning performance can be affected by morphology. Particularly important in determining turning performance is the rigidity of the body and the mobility and position of the control surfaces (e.g. fins, paddles, flippers; Webb, 1984; Weihs, 1993; Bandyopadhyay et al., 1997; Fish, 1997, 2002; Walker, 2000). For vertebrates, the possession of a flexible spine and elastic elements permits these animals to display considerable proficiency in their maneuverability. However, many aquatic animals are encased in rigid exoskeletons or shells that potentially constrain flexibility and maneuverability (Chamberlain, 1990; Walker, 2000). Flexibility allows an animal to turn in a space with dimensions smaller than the body length.

Arthropods have bodies constrained by a cuticle exoskeleton. Despite this perceived disadvantage, these animals are able to execute rapid maneuvers with higher efficiency than elicited by flexible vertebrates (Webb, 1979).

The body form of aquatic insects exhibits variation that is associated with a compromise between maneuverability and speed (Nachtigall, 1974; Ribera et al., 1997). The flexible body of damsel-fly larvae permits these insects to produce rapid-flexure maneuvers similar kinematically and hydrodynamically to the C-starts of fish (Brackenbury, 2002). These insects, like other aquatic larvae, are elongate with multiple flexion joints along the abdomen and no constraining wings or elytra, permitting extensive bending (Nachtigall, 1974; Brackenbury, 2002).

Whirligig beetles (Coleoptera: Gyrinidae) have a fixed exoskeleton that renders the body rigid and firm (Nachtigall, 1974). The majority of the dorsum is composed of the paired elytra, which flex only at the anterior joint with the thorax. The body has an oval design that is considered unstable and extremely maneuverable both at and below the water surface. The beetles propel themselves by drag-based strokes of the paddle-like middle and hind legs (Bendele, 1986). High-speed turning in tight circles is a characteristic behavior of whirligig beetles. These beetles turn to capture prey, avoid predators and

perform territorial displays (Humphries and Driver, 1967; Newhouse and Aiken, 1986; Fitzgerald, 1987). Typical circular turns have a radius of less than twice the length of the beetle (Fitzgerald, 1987). The turns are so tight that the beetle appears to be rotating with an axis extending vertically through the body.

The ability of beetles to turn at high speed suggests that maneuverability is not constrained by a rigid body. To investigate the maneuvering performance by whirligig beetles, high-speed videography was used to quantify the spatial (i.e. radius) and rate (i.e. angular velocity) characteristics of turning. Comparisons were made with available data from the literature on turning performance by animals with flexible and rigid bodies.

Materials and methods
Animals

Twenty-five whirligig beetles (*Dineutes horni* Roberts) were collected from an artificial pond located near West Chester, PA, USA. The beetles ranged in body length (L) from 10.9 mm to 13.9 mm (mean L=12.38±0.78 mm; mean ± S.D.) and in body mass (M_b) from 0.031 g to 0.098 g (mean M_b=0.0695±0.0192 g). Beetles were placed in plastic containers with moist paper towels and lids with air holes and transported to Brown University in Providence, Rhode Island, USA for testing within 32 h. Animals were allowed to acclimate to room temperature for at least one hour prior to testing.

Beetles were examined individually in a test arena. The arena was constructed from a 46 mm section of white PVC pipe with an internal diameter of 115 mm. The floor of the arena was constructed from clear acrylic plastic. Tapwater filled the arena to a depth of approximately 30 mm. Water temperature was 22°C. Swimming trials for each beetle lasted no longer than 2 min.

Data analysis

Beetles were videotaped at 500 frames s^{-1} and 1000 frames s^{-1} with a Kineview high speed video system (Model 1256P; United Technologies Adaptive, Optics Associates, Cambridge, MA, USA) equipped with a Fujinon-TV zoom lens (1:1.2/12.5–75; F=5.6; Fuji Photo Optical Co., Saitama, Japan) and videorecorder (Panasonic SVHS AG-7400). The resolution of the camera was 640 pixels× 480 pixels. The camera was positioned approximately 0.2 m below the floor of the swimming arena. A plastic 65 mm scale was floated on the water surface and videotaped prior to the swimming trials. Lighting was supplied with a single 1000 W halogen photographic light (Model 750-SG; Smith-Victor Corp., Griffith, IN, USA).

Video records were analyzed frame-by-frame with a video recorder (Panasonic AG-7300). Only those records in which the animal's body remained within a horizontal plane through the turn (i.e. no change in depth during swimming sequence) were used. The sequential positions of the leading edge of the head were recorded onto transparencies from the video monitor (Panasonic CTJ-2042R). The center of rotation of the turn was determined geometrically (Youm et al., 1978). Turning radius, R, and mean speed, U, were measured in m and m s^{-1}, respectively. Turns measured at the leading edge of the beetle were assumed to be equivalent to turns tracked at the center of mass because of the rigid body. For comparison with the turning performance by other animals, relative values of R and U were calculated by dividing by L. Centripetal acceleration, $\mathbf{a_c}$, as a multiple of gravitational acceleration (g=9.8 m s^{-2}) was computed according to:

$$\mathbf{a_c} = U^2 / Rg . \qquad (1)$$

Angular displacement was used to calculate the turning rate, ω, in degrees s^{-1}. The terms 'inboard' and 'outboard' were used to describe the orientation of the body and appendages of the beetles, such that inboard referred to structures facing towards the center of the turn and outboard referred to structures facing away from the center of the turn.

To examine the maximal turning performance by the beetles, data were expressed as maximum and minimum values, means ± 1 S.D. and the means of the extreme 20% of values (i.e. minimum radius, maximum turn rate). Choice of the extreme 20% of values was considered arbitrary but was used previously for comparisons of turning performance (Webb, 1983; Gerstner, 1999). Statistical comparisons by *t*-test were made using Data Desk version 3.0, and regression equations and correlation coefficients were computed using Cricket Graph version 1.3 software. Results were considered significant at the α=0.05 level.

Results

In a turning maneuver, a whirligig beetle sets the position of its elytra and the paddling rate of its outboard legs and its wing. As a result, the animal's turning radius, R, and its swimming speed, U, are independent variable parameters. Any correlation between R and U reflects the experimental circumstances in which the beetles find themselves. Because the beetles were examined individually in a test arena with a diameter of approximately 9 times the length of a beetle and 170 times greater cross-sectional area than a beetle, the movements of the animals can be considered to be unrestricted as to selection of R and U.

Swimming patterns

Whirligig beetles performed spontaneous rapid turning maneuvers in the test arena. A total of 119 turns were analyzed. Beetles swimming at the surface accounted for 86.5% of all turns. In one case, turning was performed underwater while the beetle had rolled 90° so that its venter was tilted into the turn, but the animal remained in the horizontal plane. In many cases, the turns were made as circles or as continuously decreasing spirals (Fig. 1). Such circles and spirals could be maintained for approximately 3–5 cycles. All curved trajectories by the beetles were executed as powered turns, whereby thrust-

Fig. 1. Turning maneuver of whirligig beetle (*Dineutes horni*) produced by rowing of the legs. The pattern of turning is indicated by the spiral waveform.
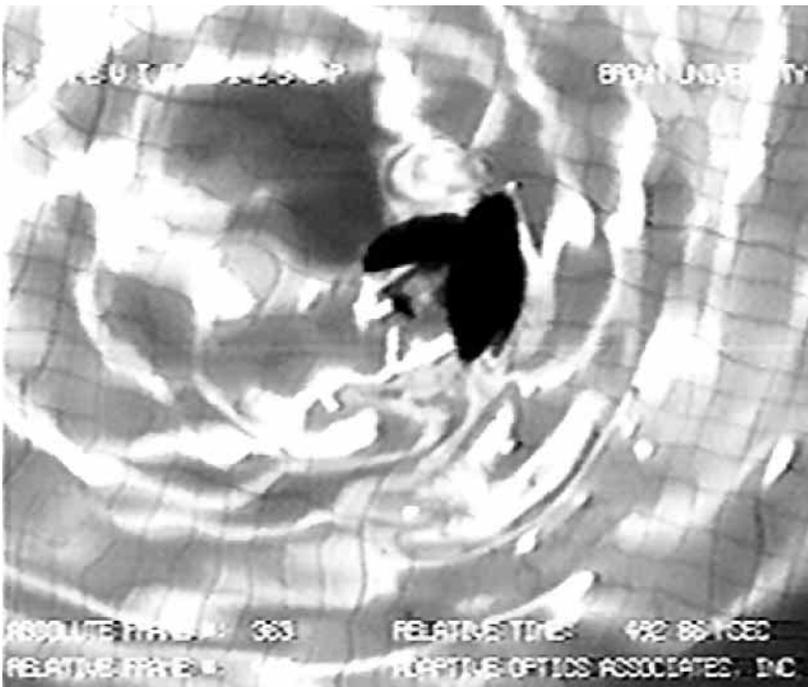
Fig. 2. Winged-propulsion by the whirligig beetle during a turning maneuver. Single frame from a high-speed video recording (1000 frames s^{-1}) shows deployment of the left wing and elytra. The beetle is turning to the left.

generating actions were continuous throughout the maneuver. Generally, asymmetrical rowing of the midlegs and hindlegs on the outboard side (i.e. the side facing away from the center of the turn) of the beetle powered the maneuver. Both

contralateral sets of legs were observed to stroke through the turn. However, the outboard legs completed the power phase of the stroke cycle more rapidly than the inboard legs. In addition, turns were effected when the foreleg on the inboard side was extended. The foreleg acted as a brake and allowed the beetle to pivot through the turn.

Turns also were observed by winged-swimming (Fig. 2). Winged-swimming was performed by sculling using a single wing (Fig. 2). This means of turning was initiated by abduction (i.e. movement away from the midline of the body) of the elytra on the inboard side (i.e. side facing the center of the turn) of the beetle to a position perpendicular to the longitudinal body. As the elytra was abducted, the underlying wing was unfolded to its full span. The elytra on the outboard side was only slightly abducted and its underlying wing was never unfolded and deployed. The inboard wing was oscillated in the space between the body and elytra at a frequency of 47.14±3.21 Hz. The distal apical half of the inboard wing acted as if jointed like a two-way hinge to the proximal part of the wing (Fig. 3). This joint midway along the wing was believed to correspond with the folding pattern of the wing (Wooton, 1981, 1992). Oscillations of the wing were synchronized with turning movements. Throughout the turn, the body showed a rotational oscillation around its center of mass. The wing was collapsed as the elytra was adducted at the end of the turn. The beetle was capable of moving in complete circles during winged-swimming.

Turning performance

Summary data on turning performance of the whirligig beetles, which was measured at the beetle's leading edge, are presented in Table 1. Turning by winged propulsion was not significantly different (*t*-test; d.f.=117; *P*>0.05) from legged propulsion for any variable of turning performance. Data for winged-swimming and legged propulsion were combined. Swimming speeds varied from 0.06 m s^{-1} to 0.55 m s^{-1} with a mean of 0.22±0.09 m s^{-1}. This range represented length-specific speeds of 4.7–44.5 L s^{-1}. Turning radius was weakly associated (*r*=0.336; d.f.=117; *P*<0.05) with swimming velocity (Fig. 4) for all data according to the equation:

$$U = 0.21 + 6.24R . \qquad (2)$$

However, when only the data for the minimum 20% of *R* were considered, no significant correlation was found (*r*=0.310;
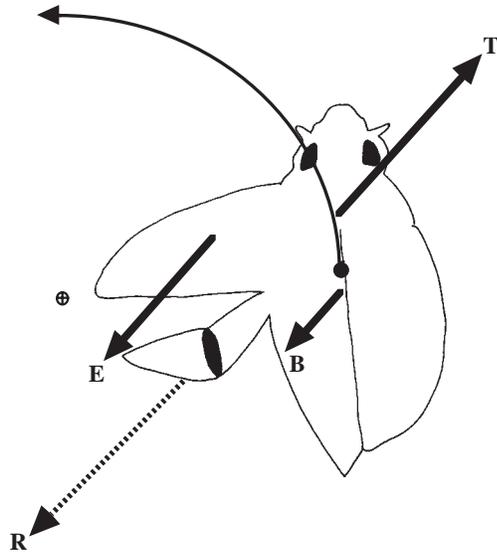
Fig. 3. Model of forces (drag, vectored thrust) resulting in turning of the whirligig beetle. The path of motion is indicated by the curved arrow from the center of mass (solid dot) around the center of rotation (circled cross). Vectors for thrust (**T**), reaction force (**R**), elytra drag (**E**) and body drag (**B**) are indicated by the straight arrows. The propulsive force (**T**) provided by the sculling of the wing results in forward motion that is biased towards the left by the asymmetry of elytra drag exceeding body drag.

Fig. 4. Relationship of swimming speed (U) and turning radius (R) for horizontal turning maneuvers by whirligig beetles. Squares and triangles represent turns produced by rowing of the legs; circles represent turns executed by winged-swimming. Triangles represent data for the minimum 20% of radii for all turns measured. The upper regression line ($r=0.336$, $P<0.05$; see text for the equation of the line) was fit to all data; the lower regression line ($r=0.310$, $P<0.20$) was fit to the minimum 20% of turning radii.

d.f.=22; $P<0.20$). Mean minimum radius was 5.1 ± 0.07 mm, which was 0.41 ± 0.06 L. The smallest relative minimum R was 0.24 L, recorded for a beetle performing a 90° turn at 0.12 m s^{-1}.

The highest turning rate (ω) was found at an R of 4.7 mm (0.38 L), and ω decreased curvilinearly with increasing R (Fig. 5). The relationship between ω and R was found to be:

$$\omega = 42 \pm 13R^{-0.77\pm0.14}, \tag{3}$$

which was statistically significant ($r=0.693$; d.f.=117; $P<0.001$). The standard error in the coefficient and, more importantly, in the exponent was included because we wished to examine any correlation between ω and $\mathbf{a_c}$ and check that correlation for consistency with equations 2 and 3. The wide variation in the coefficient and exponent reflects the breadth of maneuverability of the animal. Because $U=\omega R$, the centripetal acceleration ($\mathbf{a_c}$) in equation 1 is calculated from turning rate and radius by $\mathbf{a_c}=\omega^2R/9.8$. Turning rate and radius, however,

are themselves correlated by equation 3. Equation 3, when solved for R, yields:

$$R = \left[\frac{\omega}{(42\pm13)}\right]^{-1.3\pm0.3}. \tag{4}$$

Using equation 4 to eliminate R from $\mathbf{a_c}$ results in $\mathbf{a_c}\propto\omega^{0.7\pm0.3}$ for the range of maneuvers executed by the beetles in this study. Thus, equations 2 and 3 imply that $\mathbf{a_c}$ should be consistent with a linear dependence on ω. In this study, turning rate was linearly related to $\mathbf{a_c}$ (Fig. 6) with a significant correlation ($r=0.898$; d.f.=117; $P<0.001$). The regression equation for this relationship was:

$$\mathbf{a_c} = -0.23 + 6.63 \times 10^{-4}\omega. \tag{5}$$

Maximum ω was 4428 degrees s^{-1} with a maximum $\mathbf{a_c}$ of 2.86 $\mathbf{g}$.

Table 1. *Summary data on turning performance by whirligig beetles*

	Radius (mm)	Radius (L)	Swimming speed (m s^{-1})	Swimming speed (L s^{-1})	Centripetal acceleration ($\mathbf{g}$)	Centripetal force ($\times10^{-3}$ N)	Turning rate (degrees s^{-1})
Minimum	3.0	0.24	0.09	7.29	0.08	0.05	409.1
Maximum	31.1	2.51	0.62	50.48	2.86	1.95	4437.5
Mean	10.7	0.86	0.28	22.42	0.96	0.65	1790.2
S.D.	5.8	0.47	0.11	8.74	0.67	0.45	901.1
Extreme 20%	5.1	0.41	0.44	35.24	2.00	1.36	3168.4
S.D. 20%	0.7	0.06	0.05	4.36	0.33	0.22	495.8
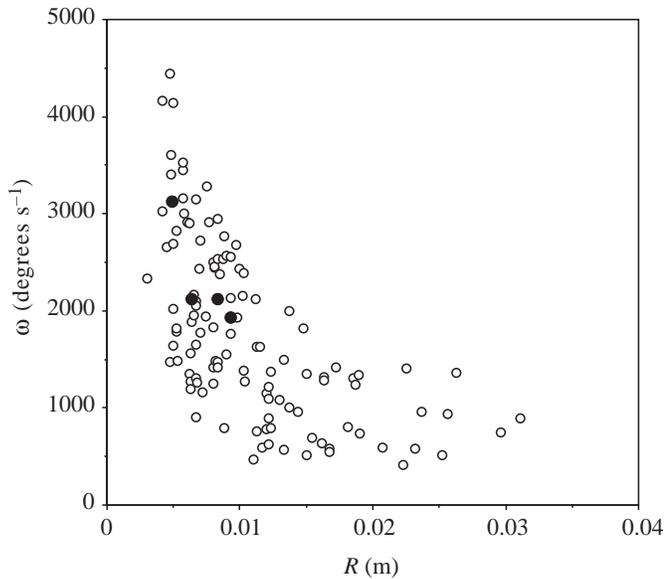
Fig. 5. Relationship of turning rate, ω, and turning radius, R. Open circles represent swimming by rowing of the legs; filled circles represent turns executed by winged-swimming.
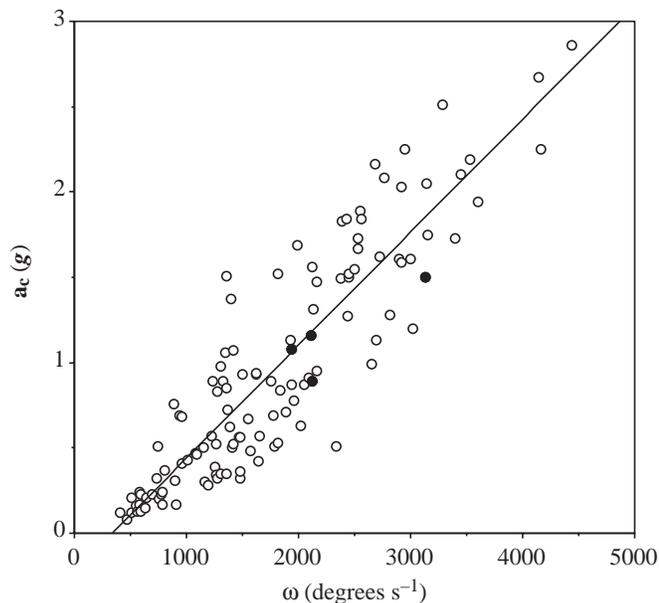
Fig. 6. Relationship between centripetal acceleration, $\mathbf{a_c}$, and turning rate, ω, for whirligig beetles. Open circles represent swimming by rowing of the legs; filled circles represent turns executed by winged-swimming. The regression line ($r=0.898$, $P<0.001$; see text for the equation of the line) is for all turns.

Discussion
Whirligig maneuvers

Whirligig beetles, as single individuals or in a group of thousands, normally swim slowly or rest on the surface of ponds or calm streams (Bendele, 1986; Vulinec and Miller, 1989; Watt and Chapman, 1998). Beetles detect prey with visual and mechanical receptors, including possible reception of reflected surface waves in a system analogous to echolocation (Kolmes, 1983). Once prey is detected, the beetle will circle the prey before capturing and consuming it. When disturbed, the beetles display a fright reaction in which the insects turn in multiple circles at high speed (Tucker, 1969). This reaction is termed 'protean behavior' (Humphries and Driver, 1967; Newhouse and Aiken, 1986), which is defined as that behavior "which is sufficiently unsystematic to prevent predicting in detail the position or actions of the actor."

Territorial behaviors, characteristic of each sex of whirligig beetle, use turning maneuvers. Spurts are typical of male whirligig beetles (Fitzgerald, 1987). A spurt is a rapid maneuver in which the beetle accelerates quickly, turns abruptly at an acute angle and then drifts. Females more commonly use whirls, which are defined by large circular or spiral trajectories. Extremely tight circular paths ($<2\,L$), known as pivots, are used by both males and females in territorial displays (Fitzgerald, 1987).

Typical turning maneuvers in whirligig beetles were shown to be powered by asymmetrical paddling of the paddle-like legs. The middle leg can paddle with a frequency of up to 25 Hz and the hind legs stroke twice as fast (Bendele, 1986). The water beetles *Acilius* and *Dytiscus* similarly steer with asymmetrical paddling (Nachtigall, 1974). *Acilius* turns with hind legs swept through greater amplitudes and frequencies. *Dytiscus* turns by varying the phase relationship between contralateral legs (Hughes, 1958). For rapid turns, *Dytiscus* can extend one hind leg to act simultaneously as a brake and pivot, while the opposite leg paddles.

The whirligig beetles of the genus *Dineutes* can reach speeds of 0.53 m s^{-1} (Tucker, 1969), although speeds of up to 1.0 m s^{-1} have been reported for the related genus *Gyrinus* (Nachtigall, 1974). The maximum U measured in this study was in agreement with the results reported by Tucker (1969) but was lower than the maximum speed reported by Nachtigall (1974). Higher speeds may have been recorded if rectilinear swimming was measured and the beetles were allowed to be heated above ambient temperature. Pond-dwelling *Dineutes* favor sunny areas, where they presumably warm themselves by basking (Fitzgerald, 1987). Higher internal temperatures can increase muscle output and locomotor performance.

The increase in ω with decreasing R occurred because, over an equivalent range of U, beetles would traverse similar arc lengths. With smaller-radius turns, beetles would move through a greater number of degrees than during larger-radius turns. ω approaches an asymptote as the beetles cannot increase U further. This limit is dependent on energetic constraints associated with the drag on the beetle and inefficiencies of the paddling mode. At high U, the beetles would experience high drag from displacement of half their body mass in water and surface tension at the water surface (Tucker, 1969). Furthermore, paddling is inefficient at high U because the speed differential between the body and the paddle becomes smaller with less propulsive force being generated (Blake, 1986; Fish, 1996).

The winged-swimming of the whirligig beetle is a unique style of locomotion that has not previously been reported for any

insect. The results reported here are the first description for an insect of winged-swimming with single wing deployment as a unique mechanism for turning. Although insects can swim using legged-propulsion or skim the water surface while in flight (Nachtigall, 1974; Marden and Kramer, 1994), winged-swimming of insects is rare and has not been analyzed. Adult female *Hydrocampa nymphaeata* (Lepidoptera) swim by a combination of wings and legs (Nachtigall, 1974). Minute aquatic Hymenoptera, including *Polynema*, *Hydrophylax*, *Limnodytes* and *Caraphractus*, swim using the wings solely (Lubbock, 1863; Matheson and Crosby, 1912). *Caraphractus cinctus* was described to swim rapidly with a jerky motion that corresponded to a wingbeat cycle of 2 Hz (Matheson and Crosby, 1912). Implicit in the descriptions of winged-swimming in insects is that both wings are deployed simultaneously.

The mechanics of winged-swimming for turning the whirligig beetle can be modeled as a combination of drag and vectored thrust (Fig. 3). In this conceptualization, the sculling by the wing could act to generate thrust at an acute angle to the longitudinal axis of the body. Both the body and the abducted elytra can generate drags. Compared with the streamlined cross-sectional profile of the body, the elytra could generate an asymmetrically larger drag on the inboard side of the beetle. Such an asymmetry of forces could generate a torque about the center of mass. Thus, in this model, the sum of all torques derived from the thrust and imbalance of drags from the body and the elytra relative to the center of mass would result in a circular motion of small radius.

Why winged-swimming is used for turns in deference to leg paddling is unknown. Wing-swimming confers no advantage in turning performance compared with paddling. The smallest radius and highest rate for a winged turn was $0.4 L$ and 3130.4 degrees s^{-1}, respectively. Theses values were not equivalent to the minimum R and maximum ω for paddling, although they were in the extreme 20% of values.

Turning mechanisms

Turning is effected by dynamic forces. These forces include unsteady inertial forces and steady non-inertial forces. Inertial forces include body internal dynamics (i.e. redistribution of body mass) and fluid inertial reaction (i.e. pulsed jet), whereas steady non-inertial forces include lift and drag. In the aquatic maneuvering systems of most animals, the non-inertial forces dominate.

Animals can use an asymmetrically applied drag from their appendages to produce a pivot point in water to rotate the center of mass of the body around it. This mechanism is analogous to using a single oar to turn a rudderless rowboat. If the rowboat has forward momentum, the inboard oar can act as a brake and develop the turning drag by being held stationary in the water. The posteriorly oriented drag is applied to the distal end of the oar creating torque to turn the boat. Alternatively, the rowboat can be turned by active paddling of the outboard oar. Sweeping the outboard oar posteriorly produces a forward directed drag at the blade, which produces a net torque to angularly accelerate the boat.

Animals that maneuver with appendages modified as paddles work well in conditions dictated by low speed and precise control (Webb, 1997). However, precise turns should be less effective in conditions of rapid movement with high speed. In instances where the inboard paddle is held stationary, the consequence of using such a drag-based maneuver is a dramatic reduction in speed because the appendage, which is typically used for propulsion, becomes a braking device without producing thrust. The energy cost of turning in this manner will be high as the animal must accelerate to restore its original speed. Speed can be maintained if the outboard appendages are continuously paddled through the turn. In this case, the active paddling motion produces the turn. This mechanism has distinct advantages when $U=0$, as the paddles induce their own speed and hydrodynamically derived drag without movement of the body (Blake, 1986). Turns can be performed in limited spaces, and turns can be composed of pure rotational movements with no body translation (Walker, 2000).

Lift-based maneuvering systems have the advantage of producing a centripetal force to effect turning without incurring a large decelerating drag (Watts, 1961). This is the primary system used by ships, fish, penguins and marine mammals (Manning, 1930; Howland, 1974; Hoerner and Borst, 1975; Weihs, 1981; Webb, 1983, 1997; Hui, 1985; Marchaj, 1988; Fish and Battle, 1995; Fish, 1997, 2002). Lift-based maneuvers work best with high aspect ratio appendages used as control surfaces. The effectiveness of lift-based mechanisms varies with speed (Marchaj, 1988). Lift used by the control surfaces to create destabilizing moments varies in proportion to U^2. However, lift-based turning is independent of speed (Webb, 1997). As speed decreases, the lift also decreases relative to the required force necessary to turn so that maneuvering is more difficult at low U.

Despite the apparent advantages of lift-based *versus* drag-based systems with regard to high speed turns, the use of rowing appendages can be beneficial for continuous turning. Propulsion is curtailed during small-radius turning maneuvers using extreme body flexibility in combination with lifting surfaces (Fish, 2002). During these turns, the lifting surfaces abandon their function as propulsive surfaces and are used as control surfaces. The turn becomes unpowered, and the duration of the turn is dependent on the momentum of the animal at the start of the maneuver. Thus, these unpowered turns are limited in duration, as frictional drag on the body causes a loss of momentum. To generate more momentum to continue a turn, flexible animals using lift-based systems would have to dispense with the unpowered turn and revert to a powered turn with its comparatively larger turning radius (Fish, 2002). Only by alternating bouts of powered and unpowered turns could a position be held and the turn sustained (i.e. circular motion). Adjustments between the powered and unpowered turns will reduce the effectiveness of the maneuver. With rowing, the appendages can continue to generate thrust to maintain the minimum turning radius for a prolonged period. Although propulsion by paddling is less efficient than oscillating a hydrofoil (Blake, 1986; Fish, 1993, 1996),

maintenance of a stable circular turn could make paddling more efficient for circular maneuvers.

Comparison of turning performance

Compared to animals with flexible bodies, the relative turning radii of whirligig beetles are constrained by a rigid body morphology. Expressed as a proportion of body length, the minimum turning radius is 0.00–0.47 L for fish, 0.24 L for penguins, 0.11–0.17 L for cetaceans and 0.09–0.16 L for sea lions (Hui, 1985; Domenici and Blake, 1991, 1997; Blake et al., 1995; Fish, 1997; Gerstner, 1999; Walker, 2000). The highest minimum turning radius for fish (0.47 L) was found for the tuna (Blake et al., 1995). These fish are thick-bodied and relatively stiff, having specialized for rapid cruising (Webb, 1984). Squids, which keep the mantle stiff, cannot produce turns of less than 0.5 L (Foyle and O'Dor, 1988). The shelled *Nautilus* can, at best, negotiate a turn of 2 L (Chamberlain, 1990). Submarines with inflexible hulls have turning radii of 2–3 L (Maslov, 1970). Encased by a carapace of thickened, suture bony plates, the boxfish *Ostracion* is not limited by stiffness. Boxfish display a minimum R of 0.0005 L (Walker, 2000), which is due largely to rotation. The ability to rotate or spin is dependent on the position of multiple propulsors located about the center of mass.

Limitations in turning performance because of body inflexibility would not appear to extend to ω. Whirligig beetles demonstrate a maximum ω that is equivalent to the maximum ω for some flexible-bodied fishes (Webb, 1983). However, turning rate is inversely proportional to L (Fig. 7); thus, larger animals turn at a slower speed than do smaller animals. From this perspective, fish demonstrate superior performance with respect to ω, because they can produce a maximum ω that is

Fig. 8. Plot of centripetal acceleration, a_c, as a function of turning rate, ω. Data from Webb (1976, 1983), Hui (1985), Blake et al. (1995), Walker (2000) and Fish (1997, 2002).

equal to that of the beetle (which is 3.5–20 times the size). In Fig. 7, which compares ω over a range of body lengths, inflexible bodies are represented by the whirligig beetle and the experimental submarine USS Albacore at the extremes of the size range. If a line is drawn between these two rigid-bodied swimmers, flexible-bodied swimmers are shown to have higher turning rates with respect to their size. The tuna approaches the line and falls far below turning rates for similarly sized fish. Meanwhile, the boxfish and squid fall to the left of the line, suggesting performance constraint due to stiffness.

Higher a_c are generated by flexible-bodied organisms compared with rigid bodies for equivalent levels of ω (Fig. 8). This is largely a consequence of the tighter turning radius of flexible organisms. For these animals that turn using lifting surfaces, the high a_c is necessary to generate sufficient centripetal force for the turn. However, high a_c are not required by the beetles. The drag-based paddling and vectored thrust mechanisms can effect turns with a pivoting action that permits a higher turning rate but with lower a_c. These mechanisms allow the beetles to turn continuously without deceleration. This enhances their ability to escape predation from animals with tighter but less sustained turning ability.

Fig. 7. Comparison of turning rate, ω, with respect to size. The line connects the beetle and submarine, which both have inflexible bodies. The value for relatively stiff tuna approaches the line. Data from Webb (1976, 1983), Hui (1985), Foyle and O'Dor (1988), Miller (1991), Blake et al. (1995), Gerstner (1999), Walker (2000) and Fish (1997, 2002).

List of symbols

a_c	centripetal acceleration
g	gravitational acceleration (9.8 m s^{-1})
L	body length
M_b	body mass
R	turning radius
U	swimming speed
ω	turning rate

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