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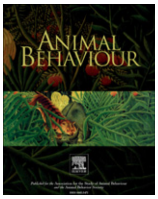

Physical constraints and the evolution of different foraging strategies in aquatic space

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Optimal balance between energy usage and feeding is crucial to an animal's fitness, and thus is a driving force in the evolution of species. Animals show varieties of different foraging strategies, each adapted to particular ecological and physical constraints. For example, while both the paddlefish and the zooplankton *Daphnia* filter-feed on patchy food sources, they differ greatly in size and in their methods of propulsion, affecting the degrees of influence of the viscous and inertial forces on these swimmers. To examine the effects of these physical constraints on the evolution of foraging strategies, we modified a recent evolution simulation designed for *Daphnia* by adding an energy penalty proportional to each turning angle used by modelled foraging agents. This modification accounts for the loss of linear momentum of larger swimmers as they change directions, directly contrasting with *Daphnia*, which, as smaller, rowing organisms, never build an appreciable momentum since they are halted by the surrounding medium after each forward stroke. While realistic random-walk-like trajectories were predicted by the simulation for *Daphnia*, distinct circling trajectories and nonzero peaks in the turning angle distributions were predicted for larger species, such as paddlefish. These results are strikingly similar to experimental data also reported here: the circling patterns and bimodal turning angle distributions observed in juvenile paddlefish.

We investigated two filter-feeding aquatic animals where one species, the zooplankton *Daphnia* sp., is the typical meal for the other species, the paddlefish. This fact is only important when one considers that it demands that the organisms live in the same environments and are subject to similar ecological conditions. Both organisms also feed on patchy food (Folt et al. 1993), yet, despite these ecological similarities, the swimming behaviours of the two organisms are remarkably different.

In general, filter-feeders collect food by straining large volumes of their surrounding medium as it flows through some part of their bodies, usually their mouth. Feeding, therefore, requires this flow, and is almost always accompanied by locomotion of some sort. While both real (Garcia et al. 2007) and modelled (Dees et al. 2008) *Daphnia* travel in trajectories resembling random walks resulting from quantifiable single-peak, zero-mean turning angle distributions (TADs), experimental and observational studies show that many constantly swimming filter-feeders travel in circular or elliptical trajectories as they feed or search for food, particularly when the food is patchy. In terms of turning angles and distributions, traversing a circle is achieved by using many consecutive positive (or negative) turning angles, resulting in anticlockwise (or clockwise) circling. Each set of consecutive positive or negative angles would appear on a TAD as a nonzero peak, strongly contrasting with the TADs of *Daphnia*.

This circling behaviour extends from smaller filter-feeding fish species, such as anchovy (Hunter & Dorr 1982), and medium-sized species, such as herring (Batty et al. 1986), to the largest living fish species, the whale shark (Nelson & Eckert 2007). The behaviour has been typically suggested to be an effective method of staying within a food-rich area. However, it has also been suggested that swimming with disorderly, random changes in direction and speed (spontaneous swimming) is more energetically costly to the swimmer than simply swimming straight ahead (Smit 1965). Smit's original findings were based on the large amounts of oxygen that spontaneously swimming fish were consuming while covering very little distance. More recently, Boisclair & Tang (1993) performed a more extensive analysis of the energetic costs of three types of swimming: spontaneous swimming, forced straight swimming and directed swimming, where the directed swimmers were trained to

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follow shadows around a circular aquarium, and therefore were constantly turning (circling) in stationary water (e.g. Muir et al. 1965). Boisclair & Tang's results showed that spontaneous swimming was 6.2 times more energetically expensive than directed swimming (circling), whereas circling was, on average, only 1.6 times more expensive than straight swimming. It is clear that there is an advantage to avoiding spontaneous swimming for larger fish, and these results have been reaffirmed by many other experiments (e.g. Weihs 1972; Weatherley & Gill 1987; Webb 1991).

Why is it, then, that of the three types of swimming mentioned above for fish, it is the very costly spontaneous swimming that most closely resembles the 'optimal' trajectories of the real and modelled *Daphnia* (Uttieri et al. 2004)? Perhaps this disparity can be explained by the method of propulsion used by *Daphnia*, one that is very different from undulating fish species. Like most zooplankters, *Daphnia* are 'rowers', meaning that they move in repeated and successive sequences of 'hops' (forward lunges), pauses and precise turns through angles that define the direction of the next hop (Pennak 1953). After each forward stroke, however, the surrounding fluid immediately stops a daphnid's motion and dissipates its kinetic energy (Videler et al. 2002). This is because *Daphnia*, being so small (on the order of millimetres), and moving at relatively slow speeds (on the order of mm/s), experience very low Reynolds numbers (Re) (Dodson & Ramcharan 1991). Re is defined as $\rho VL/\mu$, which is the ratio of the inertial (pushing) forces, ρV, to the resistive viscous forces present, μ/L, where ρ is the fluid density, V is the relative velocity, μ is the dynamic viscosity of the fluid, and L is the length of the object in motion relative to the fluid. The Re for zooplankton has been measured to be between 0.1 and 100 (Dodson & Ramcharan 1991; Videler et al. 2002; Catton et al. 2007), meaning that *Daphnia* operate in what is commonly called an 'intermediate' flow regime, where both viscous and inertial forces are relevant to the swimmer's efficiency (e.g. Daniel et al. 1992; Jordan 1992; McHenry et al. 2003). On the other hand, Re for small fish are typically one or two orders of magnitude higher than that of zoooplankton, and those of larger fish and whales are up to a half-dozen orders of magnitude higher (Videler et al. 2002). For these larger swimmers, the enormity of the inertial forces mentioned above completely overwhelms the viscous forces, introducing a dramatic contrast in the physical constraints experienced by these larger organisms and *Daphnia*.

One major consequence of this contrast is that undulators expend energy differentially while executing turns, depending on the severity of the turn (Weihs 1972, 1980), while *Daphnia* turn more freely, using rotation-like swivels, a type of movement that is uninhibited at such low Re (Videler et al. 2002). The linear momenta of larger fish are decreased as they bend their bodies through the water to turn, increasing the drag forces present on their bulky centres (Weihs 1972). To maintain speed efficiently, a fish must overcome these momentum losses with extra propulsion, which, of course, comes at a cost. Paddlefish must consider these costs at every turn, whereas foraging *Daphnia* are uninhibited while choosing trajectories.

We contend that these contrasts in physical constraints during locomotion may have been integral to the evolution of these two species. In fact, it is well known that the optimal use of resources spurs selection pressures, and therefore competition within and between species, and that this competition often shapes animals' evolved behaviours. To study the evolutionary effects of filter feeding in a patchy food environment, we recently developed an evolutionary simulation ('EVO': Dees et al. 2008) where we used the central principles of Darwinian natural selection to model the evolution of turning angle distributions (TADs) used by *Daphnia* during foraging. In the model, simulated agents foraged in a continuous two-dimensional space containing a finite circular food patch. The freely changing (evolving) parameter was the characteristic width of the TAD of the foraging agents, and the agents' fitness levels were determined by the quantity of food they gathered in a specified amount of time. The TADs of the foragers, which began as uniform, uncorrelated distributions, evolved over thousands of generations into final forms that resembled those of the real animals in both shape and width. The trajectories that resulted were also very similar to those of the real animals. Here, we more closely investigated the predictions of EVO when also considering the physical constraints encountered by larger aquatic filter feeders, such as paddlefish. Comparative analysis of the results may have significant implications regarding the possible role of physical constraints in the evolution of foraging strategies.

METHODS

Paddlefish Swimming Behaviour

Swimming behaviour was measured in 19 juvenile paddlefish, *Polyodon spathula*, with a total length of 15–35 cm. Paddlefish can be easily identified by their large, elongated snout called a rostrum. Adult fish commonly reach 1.5 m or greater in length (making their swimming habits challenging to study in captivity). The juvenile paddlefish were obtained from the Blind Pony and Hunnewell Fish Hatchery of the Missouri Department of Conservation. The fish were kept in large biofiltered and aerated tanks containing dechlorinated water raised to a salinity of 2% by the addition of stock salt (Gunther Co., St Louis, MO, U.S.A.). Fish were fed daily and kept under a 12:12 h light:dark regime. All experiments were conducted in compliance with the guidelines of the Institutional Animal Care and Use Committee of the University of Missouri at St Louis (protocol number 07-06-05). The animals were later used for either electrophysiological or anatomical studies at the university, and therefore were never released.

To record their swimming activity, individual fish were transferred to a rectangular monitoring tank of 1 × 1 m or 1 × 1.5 m. A video camera was placed above the tank and the fish were monitored for 10–120 min. Videos were directly digitized by a computer at a rate of 1 frame/s and at a resolution of 320 × 240 pixels. The swimming path was determined by the program Vidana (http://www.vidana.net). Each frame of the video was analysed automatically by tracing the outline of the fish and calculating the centre coordinates and direction (heading) of the fish. Thus, for each frame, the coordinates (x, y) were recorded. These data were further analysed with the software Igor 6.0 (Wavemetrics, Inc., Portland, OR, U.S.A.). The heading of the fish was determined as the vector from one position (centre coordinates) to the position 1 s later. The angle between successive heading vectors was defined as the turning angle. Turning angles were plotted as a function of time; histograms of turning angles were also generated.

Daphnia Model

The algorithm we used for the competitive development of the *Daphnia* TADs was identical to that used in EVO (see Supplementary Material in Dees et al. 2008). However, in the present study, we adjusted five parameters for increased precision: (1) angular space was discretized by dividing it into 200 bins, (2) the radii of the circular food patches, R, were 100 units, (3) the simulated agents travelled for $N = 2000$ unit-length steps while feeding, (4) the inheritance value, h, was set at 1/50 (representing a 2% change in the TAD from generation to generation) and (5) the TADs were evolved for 100 000 generations. As in the previous model, 20 agents competed in each generation, and the technique of destructive foraging (Viswanathan et al. 1999) was again utilized.