

A general law for animal locomotion?

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The propulsion system of animals that fly or swim are quite different from each other in their morphology and function, yet the propulsive efficiency could be maximized by a surprising similarity in the fine tuning of flapping frequency, amplitude and forward speed, according to a new study by Taylor *et al.* This conclusion was based on an analysis of the Strouhal number, which is a dynamic similarity index relevant to propulsion that relies on vortex shedding for thrust generation. Such fine-tuning of the propulsive system suggests possible consequences for physiological and ecological adaptations related to, for example muscle operating frequency and optimal speed of muscle contraction.

Evolutionary biology is the search for general patterns and constraints that govern adaptation of size, structure and behaviour, whereas biomechanics is a science where biology meets physics and where biologists profit from research on, for example fluid dynamics, and where evolutionary adaptations illustrated by nature can provide hints and solutions for engineers who want to design nature-inspired devices. Animal locomotion is a field where the optimality approach to evolutionary biology has its strongest applications, because physical laws provide both the opportunities and constraints for organismal functional design. The properties governing animal locomotion can often be characterized by an appropriate 'dynamic similarity index', where similar numerical values of the index indicate that forces acting on animals of different scale are comparable. A dynamic similarity index applicable to oscillating propulsion is the Strouhal number (St), defined as

$$St = fh/U,$$

where f is the flapping frequency, h is the peak–peak tip amplitude of oscillating appendages (fins and wings) and U is the forward speed [1]. A high St means that the wings move up and down a lot at a high frequency but a low forward speed, whereas a low St represents a more shallow wingbeat at low frequency and fast forward speed. The range of St for cruising swimmers, for example, is confined to the range $0.2 < St < 0.4$ [2], where the propulsion efficiency is maximized. Propulsion efficiency is defined as the power output:power input ratio that generates a vortex [3–5]. Locomotory propulsion by oscillating flukes or wings is generally characterized by the periodic shedding

of wake vortices that induce jet flows that carry the momentum associated with force generation (Figure 1).

In a recent study by Taylor *et al.* [6], these results from swimmers are extended to animal flyers. Taylor *et al.* compiled St from published sources providing the necessary data to calculate St and found that animal flyers show St falling in the range $0.2 < St < 0.5$ (mean $St = 0.3$), even though the size range of the species (moths, locusts, birds and bats) included span three magnitudes. This striking congruence in St among animals using cyclic oscillating foils (fins, flukes or wings) suggested to Taylor *et al.* [6] that locomotion systems are finely tuned by natural selection to a narrow range of St because this maximizes

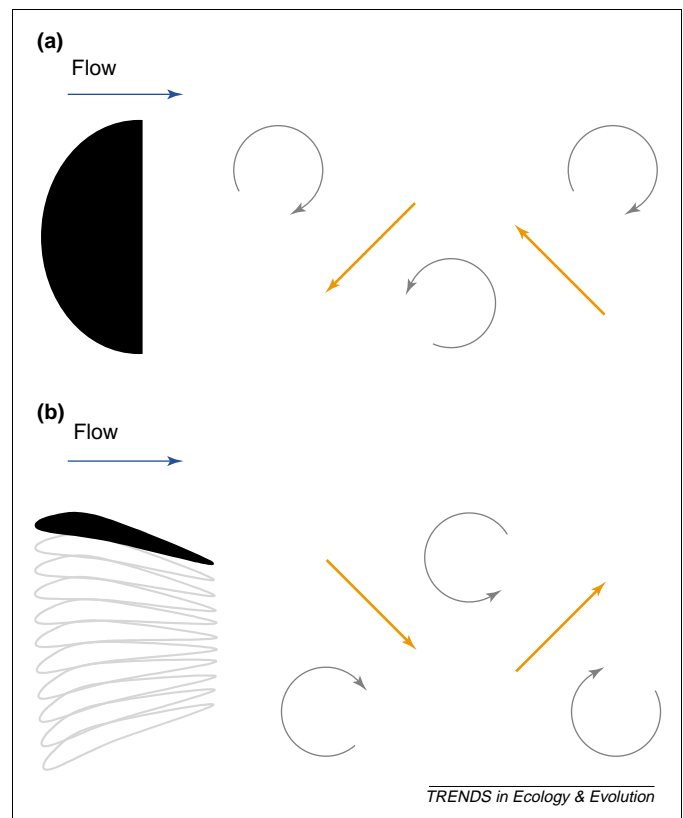


Figure 1. Drag and thrust wake vortices. (a) Bluff bodies, such as a half-cylinder (black semicircle) shed two rows of alternately rotating vortices, which interact to induce a jet that is opposite to the direction of the flow, as indicated by the red arrows. The induced jets have a directional component against the overall flow direction, and so the body will experience a reaction force aligned with the overall flow (to the right), which is why this wake is drag wake. A drag wake is also called a von Kármán vortex street. (b) An oscillating foil, such as a heaving and pitching wing or fluke, generates wake vortices rotating in opposite directions compared with the drag wake, and is therefore also called a reverse von Kármán wake. The vortices induce jet flows with a component aligned with the overall flow direction and so the body (foil, fish or bird) will experience a reaction force against the flow direction, which is a thrust propelling the body through the fluid.

propulsion efficiency. The observed pattern could have been statistical coincidence, and so Taylor *et al.* also performed a Monte Carlo analysis, where separate regressions between $\log(f)$, $\log(U)$ and $\log(h)$ against \log (body mass) were used to calculate fitted values for each species. Residuals from each of the regressions were then randomly allocated to each species without replacement to generate 50 000 new sets of St numbers. The resampled data had significantly higher standard deviation of St compared with the measured St , hence indicating selection on St to a narrow range. There are also interesting differences in St among flying animals, such that continuously flapping birds show a rather low $St \approx 0.2$, whereas birds using bounding flight and bats have $St \approx 0.4$. The data analyzed by Taylor *et al.* [6] come from various sources using different methods of measuring flight kinematics, such as video filming birds in nature to wind tunnel experiments using trained birds. Sometimes the amplitude was not given directly but derived from stroke angle and wingspan, which will overestimate St in those species. This means that the data probably contain more scatter than if all species had been studied under identical conditions.

Fluid dynamics of animal propulsion

The experimental results on hydrofoils (model fluke or fin) are from heaving and pitching foils [2,4], mimicking the movement of a fish caudal fin or the fluke of a whale, whereas birds have a flapping wing that rotates around the shoulder joint (root flapping). Flapping wing elements thus experience different local speeds relative to the air depending on location along the wingspan. To check whether this changes the pattern of vortex shedding, Taylor *et al.* [6] compared the wakes of root flapping and heaving hinged flat plates in a wind tunnel using smoke streaks. They found that the wake vortices were similar in the root flapping and heaving hinged flat plates at comparable St . Hence, the comparison between swimmers and flyers was considered justified.

Researchers have previously claimed that swimmers have a limited range of St because, in this range, propulsion efficiency is maximized [4], which has been found in heaving and pitching hydrofoils [3], and has also been confirmed by theoretical analysis of such motion in air [7]. When operating at the optimum efficiency, the foil generates one vortex at each half-stroke, resulting in a thrust wake, where vortices of alternating circulation are shed at the turning points of the oscillating foil (Figure 1b). The vortices induce a jet, which is the origin of the thrust force (Figure 1b). The reason for an optimum at $St \approx 0.3$ is that the spacing between the shedding of vortices is sufficiently large to avoid adverse interaction between consecutive vortices, and the frequency is high enough to maintain a large thrust. This tradeoff determines the optimum frequency. From a propulsion efficiency viewpoint, the important point is that each vortex yields maximum impulse (and hence thrust) for a given amount of energy input [5]. If frequency is reduced vortices will be spatially separated and adverse interaction among them is avoided, and hence there should be a weaker lower bound for St . The main selection pressure should rather be on an

upper bound for St , where adverse vortex interaction is more likely to occur.

Prospects and unanswered questions

If proved true, the claim that animals operate at some optimal frequency (i.e. St) will certainly be a unifying law of locomotion. Taylor *et al.* [6] point out that it is only at cruising speed that performance is tuned for maximum efficiency. Slow flight and hovering do not generate St in the range 0.2–0.4, because, as speed decreases, St increases. In the case of hovering, the speed will be zero and St as defined here will approach infinity. At these high St numbers, we would expect the energetic cost of flying to be high because the vortices that provide lift and thrust would interact adversely. However, hovering in hummingbirds and insects is not associated with elevated energy costs [8,9], and so adverse vortex interaction does not seem to be a problem. An efficient hovering animal generates an induced downwash, which might result in sufficient vortex spacing.

Among birds and bats representing different flight styles, from continuous flapping to intermittent and bounding flight, the variation in St is 0.2–0.5 that is a 2.5-fold difference. If these modes of flight represent different optima or different location on an adaptive envelope (or ridge in the adaptive landscape) remains unclear. Also, whether the observed range in St represents an optimum in St is a question for further investigation. One would probably have difficulties arguing that a range of a factor of two in some morphological character, for example body length in hominids, would indicate a finely tuned optimum to a life on savannahs. However, the resampling analysis indicated stabilizing selection on St , which in turn suggest that flying birds have limited permissible design options.

In a general sense, flying vertebrates should be more alike than for example non-flying mammals, which is probably true (compare the anatomical differences among a gorilla, a gazelle and a seal versus a sparrow, a hawk and an oystercatcher; ref. [10]). Recent flow visualization experiments revealed that wakes of birds are complex structures [11], and it is unclear whether the continuous vortices typical of cruising birds are compatible with the thrust wake required for maximum propulsion efficiency (Figure 1b). And what the propulsion efficiency as defined above really is for flying birds is unknown. Cruising birds are generally thought to maximize the lift:drag ratio, which gives the lowest cost of transport (energy per unit distance). It would be very interesting to clarify if maximum lift:drag ratio coincides with the maximum propulsion efficiency, or if they represent functionally different optimization criteria for flapping kinematics. Finally, the suggestion that cruising flyers and swimmers are selected to operate at a certain St poses physiologists with an interesting question, namely, is the muscle contraction frequency tuned for maximum conversion efficiency coinciding with optimum St ? Hence, as usually is the case with a new finding, it poses many questions that deserve attention and provides many new research opportunities.

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Disease dynamics: all caused by males?

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Some host individuals tend to acquire parasites at a much faster rate than do others – a consequence of heterogeneities in susceptibility and/or exposure. This is termed ‘overdispersion’ and, as for many other statistical phenomena, the degree of overdispersion often conforms to a 20/80 rule, where 20% of the host population is responsible for ~80% of the parasite transmission. But which are the hosts driving so much of the dynamics of an infectious disease? If host individuals at the tail of the frequency distribution can be identified by some common label, controlling parasitic diseases would be much easier. In two recent papers, Perkins *et al.* and Ferrari *et al.* have shown that male hosts are much more important than female hosts in the transmission of parasites.

Identifying groups of hosts that are the main transmitters of an infectious disease has always been at the center of epidemiological research. Most studies have been concerned with how gender might affect susceptibility to parasites, but, in two recent papers, both Perkins *et al.* [1] and Ferrari *et al.* [2] focus on the role of host sex in transmission. Because it is highly likely that the individuals that acquire most of a disease are the same as those who are transmitting it, these two questions are closely linked. Theory suggests that males should be more susceptible to parasites than are females, for many reasons. Among vertebrates, the male hormone testosterone is believed to have a negative effect on immune function [3,4] (but see [5]), leading to the prediction that males have higher parasite infection levels than do females. Another and simpler hypothesis, at least among mammals, is that the larger bodies of males make them easier targets for

parasites [6,7]. However, among most non-mammalian taxa, this sex dimorphism is often reversed, suggesting that females would be the most heavily parasitized sex. Moreover, invertebrate taxa, such as insects, do not have testosterone. Both these hypotheses are therefore restricted to certain taxa. A more general prediction is based on an assumed dimorphism in life histories of males and females. The so-called Bateman’s principle suggests that females maximize their fitness by investing in longevity, whereas males invest more in mating success [8,9]. Therefore, assuming that immunity is costly, females of any taxon should invest more than do males in their immune function.

The current evidence for male biases in parasitism is rather thin, except for higher vertebrates [10,11] and even here the differences are small. The lack of any general trend in other taxa could be due to few available data, or to the fact that Bateman’s principle refers to investment in immunity, which is not necessarily correlated with infection levels of parasites (e.g. owing to differences in exposure). However, Perkins *et al.* and Ferrari *et al.* [1,2] demonstrate that, even with rather small or no significant differences in parasite loads between sexes, one gender might still be far more important in spreading a disease than is the other.

Both papers (from the same research group) deal with parasites of the yellow-necked mouse *Apodemus flavicollis*. This rodent is a crucial host in maintaining tick-borne encephalitis, a viral disease of humans that occurs in many parts of Europe and Asia. Ticks act as both vector and reservoir hosts for the virus, and the main hosts are small rodents. Humans are accidental hosts and become infected through tick bites. In the study by Perkins *et al.* [1], the potential for transmission could be determined because the hosts carried specific co-feeding groups of ticks, where

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