CHICAGO JOURNALS

The American Society of Naturalists

Why the Wheels Won't Go
Author(s): Michael LaBarbera
Source: *The American Naturalist*, Vol. 121, No. 3 (Mar., 1983), pp. 395-408
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/2461157
Accessed: 29/12/2008 17:43

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=ucpress.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

The University of Chicago Press and *The American Society of Naturalists* are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

http://www.jstor.org

Vol. 121, No. 3 The American Naturalist March 1983

WHY THE WHEELS WON'T GO

MICHAEL LABARBERA

Department of Anatomy, University of Chicago, 1025 East 57th Street, Chicago, Illinois 60637

Submitted November 10, 1981; Accepted September 3, 1982

Why don't animals have wheels? Introductory biology teachers commonly note the lack of rotating structures in biological systems, usually as a starting point to illustrate the restrictions that structure and physiology place on the forms which may arise via natural selection. The question of why animals do not have wheels is part of the professional folklore of biology; while rarely addressed in the formal scientific literature, every biologist is familiar with the question and has a favorite set of explanations.

This question has recently been raised in a popular context by Gould (1981). Gould points out that the conventional wisdom on the absence of wheels in nature can no longer be strictly upheld; recent work on the mechanisms and structure underlying the action of bacterial flagella (see Hilmen and Simon 1976) has shown that a rotating wheel and axle structure does indeed exist in nature. However, the diffusion-based transport which activates this system only reinforces the traditional wisdom on the difficulty of supplying nutrients to a rotating system (Gould 1981).

Gould also points out that the wheel has not been universally preferred as a mode of transportation, even among human cultures familiar with the concept. The best documented example of this is the replacement of wheeled vehicles by camels in the Middle East and northern Africa between the second and the sixth centuries as a result of the deterioration of Roman roads and the lower efficiency of wheeled vehicles on rough terrain (see Bulliet [1975] for a full treatment of this topic). Despite this historical counterexample, Gould (1981) retains faith in the concept of wheeled vehicles as the epitome of efficient transport and asserts that "wheels are not flawed as modes of transport; I am sure that many animals would do far better with them" (p. 44).

The persistence of the idea that wheels represent a generally superior mode of transport prompts the present discussion. If wheels are best, the dearth of rotating systems in biology must be ascribed to some intrinsic limitation on biological systems; the limitation usually cited is a purported difficulty in supplying nutrients through a rotating joint. I believe the concept of the general superiority of wheels as a mode of transport is false and the limitation which constrains the evolution of

Am. Nat. 1983. Vol. 121, pp. 395–408.

such systems is extrinsic to biological systems per se, lying instead in the limited utility of rotating systems in most natural environments.

The advantage of rotating systems for transportation is primarily an energetic one; when traveling at a constant speed, the kinetic energy of such a system remains constant, while the systems found in nature such as the stepping cycle in tetrapods or the oscillation of a fish's tail involve continual accelerations and decelerations of portions of the organism's body. However, this energetic advantage of rotating systems arises only in a limited range of circumstances, and as I will show here, the restrictions on the utility of the wheel (or rotating systems in general) as a form of transportation are severe. Careful analysis of these restrictions allows the identification of environmental settings in which rotating systems do indeed have advantages as a form of transportation and the general characteristics organisms must have to use such systems. By knowing where to look and what to look for, it is possible to identify two large and diverse groups of organisms in addition to bacteria which do use the principle of the wheel for transportation.

To be as general as possible, this discussion will analyze the potential of all rotating systems (not only wheels) for transportation of organisms. In terrestrial systems, I will attempt to evaluate the potential of both wheels *sensu strictu* and rotating cylinders and spheres for transportation (although I will refer to all of these systems as "wheels"). In aquatic systems I will treat both the known rotational system, bacterial flagella, and the potential of other rotating systems such as an axle and propeller. I will ignore rotating systems which are not used for transportation through the environment external to the organism. For example, although the crystalline style of bivalved molluscs does rotate and, by acting as a windlass, transports strings of food-laden mucus into the gut, such internal systems will not be addressed. In both terrestrial and aquatic systems I will analyze the relationship between size and utility in rotating systems, an important topic which has been previously ignored.

AQUATIC SYSTEMS

The bacterial flagellum.—The motor which drives the bacterial flagellum is the only true wheel and axle structure known in biology. Although the details of its mechanism are not known, the general structure has been well established (Adler 1976; Hilmen and Simon 1976) and there is no question that the flagellum is indeed rotated as a whole (Silverman and Simon 1974). In order to understand the potentials and limitations of such a system, it is necessary to consider the physical phenomena which convert flagellar motion into thrust.

The physical phenomena important in any motion through a fluid can be identified to a first approximation by the value of a dimensionless index, the Reynolds number (Re). The Reynolds number is defined as $\mathrm{Re} = \rho UL/\mu$, in which ρ is the fluid density, U is the velocity of the body relative to the fluid, L is a characteristic length of the body, and μ is the dynamic viscosity of the fluid (see Vogel 1981). In more intuitive terms, the Reynolds number represents the approximate ratio of inertial forces (the numerator) to viscous forces (the denominator) in any flow situation in which the object is completely immersed in the fluid.

Cilia and flagella operate in a very low Reynolds number regime (Re = 10^{-5}–10^{-6}) where viscous effects predominate. This is a situation not at all familiar to organisms such as humans whose experience with fluid movement is exclusively in high Reynolds number situations. At low Reynolds numbers (Re < 1) inertial effects are negligible and all motions of both the body and the fluid are strictly reversible. Humans tend intuitively to superimpose high Reynolds number explanations on low Reynolds number situations; one's first impression on viewing a flagellum is that it acts rather like a fish's tail (when the flagellum waves sinusoidally in a plane, as in most eukaryotic flagella) or like a corkscrew pulling itself into a cork (when moved in a three-dimensional helix as in the bacterial and some eukaryotic flagella). But at low Reynolds numbers, the inertial effects on which these mechanisms depend are far outweighed by the effects of fluid viscosity; if a bacterium cruising at 30 μm/s stopped its flagellum instantaneously, it would coast to a halt in less than a tenth the diameter of a hydrogen atom (Purcell 1977).

At low Reynolds numbers, imparting momentum directly to the fluid by throwing it away is difficult; paradoxically, thrust production by cilia and flagella is dependent on drag, specifically on the variation of drag of a cylindrical object with its orientation relative to the flow. At Reynolds numbers less than unity, the drag of an elongated cylinder moving at a given speed parallel to its long axis is approximately twice that of the cylinder moving perpendicular to its long axis (see Wu 1977; Vogel 1981). The drag force in each situation is given by $F_D = C_D UL$, in which F_D is the drag force, U is the translational velocity parallel to the given axis, C_D is the appropriate drag coefficient, and L is the length of the flagellum (Wu 1977). If a cylinder is moved at some angle through a fluid at low Reynolds numbers, the flow relative to the cylinder may be resolved into its parallel and perpendicular components. Given the dependence of drag on orientation of the cylinder, the net drag force will not be oriented at 180° to the direction of motion, but at some smaller angle. This net drag force may in turn be resolved into a component opposing the motion of the cylinder and a component perpendicular to the line of motion of the cylinder. The latter component, although induced by drag, represents a thrust. Whenever a cylinder at low Reynolds numbers is moved through a fluid at some angle between 0° and 90° to its longitudinal axis, a net thrust will be produced; this principle underlies the action of all cilia and flagella (see Wu 1977).

A cylinder moved in a helicoidal path (such as a bacterial flagellum) is, in one sense, a more efficient way of producing thrust than a cylinder moved in a plane sinusoidal path (such as most eukaryotic flagella). The former will generate thrust continuously along its length, while the latter will generate no thrust on the portions of the cylinder at the crests or troughs of the waves, since in these regions the motion of the cylinder relative to the fluid is parallel to the cylinder's long axis. This difference may be reflected in the generally higher swimming speeds (for a given body size) of prokaryote over eukaryote flagellates (Sleigh 1978); however, given the very low absolute efficiency of the bacterial flagellum at converting input power to thrust, about 1% (Purcell 1977), this difference is probably not significant.

A detailed analysis of flagellar thrust production and efficiency is complicated considerably by the torque produced by a flagellum moving in a helicoidal path, since this torque must be opposed if a net thrust is to be generated. More complete treatments of this topic and discussions of some of the complexities of flagellar locomotion glossed over here can be found in Wu (1977), Holwill (1977), and Holberton (1977). Note that the utility of the rotating bacterial flagellum is ultimately dependent on the difference in the drag of a cylinder in various orientations relative to the flow; the fact that the system involves rotation is of secondary importance. It is also important to note that a classical propeller (a rotating airfoil or hydrofoil) would be useless in such a low Reynolds number situation, since thrust production of a propeller is dependent on inertial effects in the fluid.

The propeller.—An angled moving cylinder is one of the few effective thrust production devices at low Reynolds numbers (see Vogel 1981), but other devices are more efficient at higher Reynolds numbers when the importance of viscous effects decreases. In other words, angled cylinders will become relatively less efficient as either speed or size increases, and at higher Reynolds numbers ($\mathrm{Re} > 1$), the undulatory propulsion typical of fish seems to be the preferred mode of thrust production in biological systems. But why has no organism with a bacterialike rotary motor evolved an analog to human technology's solution for thrust production at high Reynolds numbers—the propeller?

Most propellers in use on ships are about 60% efficient at converting input power to thrust (Streeter 1966). This rather low efficiency is dictated by the maximum acceptable tip velocity of the propeller; if the tip velocity of the propeller is too high, the water tends to cavitate, resulting in a loss in thrust and mechanical damage (erosion) to the propeller. Even in a medium such as air where cavitation, per se, is not a problem, the maximum efficiency of a propeller is limited. The maximum efficiency for a typical airplane propeller is about 80% (Rouse 1946). Considerable effort and ingenuity were expended to optimize the design of the propeller for the human-powered aircraft, the *Gossamer Condor*. The maximum efficiency of this propeller is about 88% (Larrabee 1980).

Propulsive efficiencies of 60%–80% appear to be good, especially in relation to the 1% efficiency of the bacterial flagellum. As meritorious as these figures are, one can do better. Katz and Weihs (1978, 1979) analyze the hydrodynamics and efficiency of an oscillating flexible foil, analogous to the caudal fin of fish and, perhaps, bird wings. Although similar previous calculations on a rigid foil yielded an efficiency about the same as that for airplane propellers (Scherer 1968), oscillating flexible foils can far exceed this efficiency, reaching values of 96%–98% (Katz and Weihs 1979). This potential propulsive efficiency can be achieved in practice. The efficiency of a fish's tail is a function of fish size (i.e., Reynolds number); efficiency increases rapidly with size and asymptotes at about 96% (Webb 1977).

In light of the wide gap in attainable propulsive efficiencies between rotating propellers and oscillating flexible foils, natural selection should favor the oscillating tail for its energetic savings alone. Whether it is possible to evolve some way of supplying nutrients to a rotating system is beside the point; oscillating systems may evolve in a more straightforward fashion and pose overwhelming energetic advantages.

In summary, in aquatic systems at Reynolds numbers less than one, rotating systems have marginal advantages. At Reynolds numbers greater than one, they are at a serious disadvantage relative to more easily evolved systems. In this case, the lack of natural rotating systems is no surprise, since there is no energetic or structural basis on which natural selection would favor such systems.

TERRESTRIAL SYSTEMS

The wheel: general advantages and limitations.—Even the most ardent admirers of wheeled transport will admit that there are some modes of life in which wheels seem not to be very useful. For both arboreal and fossorial animals, wheels are clearly inappropriate. It is difficult to conceive of a locomotory system involving wheels which would function at all in these situations; certainly grasping implements such as paws or insect legs or a combined locomotion and adhesion system such as that found in terrestrial gastropods (Denny and Gosline 1980; Denny 1981) are necessary for animals living in bushes or trees. For burrowing, hydrostatic animals such as lumbricid worms seem nearly ideal given their abilities to (1) exert high forces both laterally and anteriorly, (2) involve nearly all of the body musculature in generating these forces, and (3) transfer reaction forces to the earth through most of their body's length, thus avoiding high local shear stresses (Trueman 1975). However, hydrostatic systems do not scale well. The Law of LaPlace ($T \propto PR$, in which T is the wall tension, P is the internal pressure, and R is the radius) and the finite strength of the body wall apparently limits the maximum radius of such systems (see Jones 1978); the giant earthworms of Australia (genus *Megascolides*) may be 3 m long but are only about 1 cm in diameter (Barnes 1974). For large burrowers, legs with strong claws enjoy many of the same advantages as hydrostatic systems. It should be noted that wheeled mining machinery, although physically underground, excavates large quantities of material in order to create a local environment which is more similar to surface conditions than to animal burrows.

Wheels, then, are basically restricted to use on the surface of the ground, and seem to be an excellent mode of transport in this habitat. For humans, the wheel (in the form of a bicycle) can be the most energetically efficient mode of transportation (Wilson 1973), surpassing both walking and motorized transport. To take a more extreme example, the cost of locomotion is lower for paraplegics confined to a wheelchair than for healthy humans walking (Peizer et al. 1964; Voight and Bahn 1969). This observation is particularly impressive in light of the increased mass involved (the wheelchair), the use of weaker sets of musculature (arm and pectoral muscles), and the reduced stamina of paraplegics (Voight and Bahn 1969).

A paradox arises here. Bicycles were first built about 1816, and the bicycle in its modern form dates from 1885 (Wilson 1973). User-propelled wheelchairs date from about 1655 (Burdett et al. 1977; Kamenetz 1969), and the wheelchair in its modern form dates from the mid-1800s (Kamenetz 1969). Given the energetic advantages of these two forms of wheeled vehicle and the fact that both have been available for about 100 years, why are they not more popular as a habitual form of transportation? This question may appear to be frivolous, but the fact that it appears frivolous is, in itself, significant. The general populace does not travel in wheelchairs or on bicycles as they go about their daily tasks because wheelchairs and bicycles are an awkward mode of transportation of limited maneuverability, to which a 15-cm curb can represent a major barrier. This trivial observation is precisely the point of interest in this discussion: Wheels are a highly efficient mode of transportation, but only on unrestricted and flat terrain.

The wheel on irregular terrain.—Wheeled vehicles which depend on friction with the ground for driving force cannot surmount any vertical obstacle higher than the radius of the wheels (Bekker 1956). Smaller obstacles can still represent a major barrier; the skill necessary to negotiate a curb unaided in a wheelchair deserves considerable respect, involving as it does controlled shifts in the center of gravity and rather precarious balancing to elevate the front wheels above the curb (Kamenetz 1969, pp. 167–170). It is reasonable to assume that a hypothetical animal with wheels would be able to duplicate these gymnastics. In the absence of the ability to shift the center of gravity, Bekker's (1956, pp. 381–387) analysis indicates that the maximum height of obstacles which could be negotiated would be about one-fourth the wheel diameter (assuming a coefficient of adhesion of 0.7 and four-wheel drive; half this for two-wheel drive). Regardless of the ability to shift the center of gravity, an obstacle half the diameter of the wheels (or the larger wheels, if diameters differ) still remains an absolute barrier.

The relationship between wheel diameter and the height of obstacles which can be surmounted poses serious limitations for the utility of wheels as a general mode of transportation. That this limitation is not immediately obvious is primarily because common, wheeled vehicles such as farm carts, bicycles, and automobiles use relatively large diameter wheels on prepared terrain such as roads and sidewalks. Readers who doubt this relationship should try pushing a common laboratory cart down a city sidewalk, or cross a curbed street with a baby pram. This relationship was more obvious to our ancestors. Initial settlement patterns in the United States were determined by the availability of waterways and good trails (Meyer 1917), and the value of a good road could be realized in direct monetary terms by those who controlled it. (A "turnpike" was originally a privately constructed road; access to a prepared road was valuable enough to be worth a fee.)

Bekker (1956, fig. 169) implies that the distribution of irregularities on natural terrains is log normal; small irregularities are far more common than large ones. Wong (1978) presents data that show that the profile of natural terrains can be adequately represented as a function where the frequency of occurrence of an irregularity is inversely proportional to its wavelength; again, small irregularities are far more common than large ones. Given the fact that, on natural terrains, the topography becomes increasingly irregular as the scale of interest decreases, the limited ability of wheeled vehicles to surmount obstacles would seem to set a lower size limit to the diameter of a wheel to be used for transportation. Without more detailed information on the frequency distribution of irregularities as a function of size on natural terrains, where exactly this limit lies must remain vague. I believe an all-terrain roller skate is a physical impossibility; certainly an antlike organism with wheels 2 mm in diameter would be unable to leave its nest without stalling on sand grains, pebbles, and fallen grass blades. On natural substrates, there are thus scaling limitations to the utility of wheels, with smaller wheels being at an increasing disadvantage in mobility. These problems may be reduced by decreasing vehicle weight to make it easier to surmount obstacles, since the total weight which must be raised in elevating the center of mass will be lower. In the biological literature, these scaling limitations to the use of wheels have been alluded to only by Went (1968) and he, unfortunately, did not point out the physical basis for this limitation.

Ability to deal with obstacles and ditches would be particularly important on discontinuous terrain, and no wheeled vehicle will ever be able to equal the observed performance of mountain sheep on a hillside, where the "ditches" leaped may be 14 m across and the flat terrain on the opposite side of the chasm only 20 cm wide (see Gambaryan 1974, p. 105).

The wheel on compliant terrain.—Once one abandons rigid substrata such as asphalt or concrete, other limitations on wheels become apparent. For example, the lower cost of transport for wheelchairs versus walking cited above is valid only on hard surfaces; on compliant substrates this advantage disappears. Wolfe et al. (1977) investigated the cost of locomotion for paraplegics in wheelchairs on a concrete sidewalk covered with "standard, synthetic, indoor-outdoor carpeting" (p. 1023) with a 0.64-cm bonded foam pad. Under the latter conditions the cost of locomotion increased by 36%–56% over that on a concrete surface, values which exceeded the cost of locomotion for walking. These results are reflected in the recommended standards in the United States for buildings to allow maximum access to the handicapped: If carpeting is necessary, a tight, dense loop pile without padding is recommended (Miller 1973; Anonymous 1975). Given the generally similar costs of transport for walking animals regardless of the number of legs (Herreid et al. 1981), these results should be generally applicable to a comparison between wheels and legs as a mode of transport.

According to Bekker (1956), rolling resistance of wheels increases with increasing soil compliance; Wong (1978) presents data showing that rolling resistance of "medium hard soil" can be 5–8 times that on concrete and rolling resistance on sand can be 10–15 times that on concrete. Wong (1978) also indicates that the proportional differences in rolling resistance increase with decreasing wheel diameter, i.e., the cost of transport on natural terrains is increasingly sensitive to substrate compliance as the diameter of the wheels decreases. For large-diameter wheels, width of the wheel has little influence on rolling resistance (thus traditional large-diameter, narrow-width wagon wheels are well designed), but for small wheels, increasing width decreases the rolling resistance on compliant terrain (Bekker 1956; Wong 1978). Decreasing vehicle weight also decreases the importance of substrate compliance and thus decreases rolling resistance (Bekker 1956).

In summary, on natural surfaces wheels lose much of their advantage in terms of cost of locomotion. Large diameter wheels should be narrow, small wheels should be as wide as possible to minimize rolling resistance. As was the case for irregular terrain, vehicle weight should be minimized.

The wheel on cluttered terrain.—The final factor which must be analyzed in determining the utility of wheels as a form of transportation for organisms is the maneuverability of wheeled vehicles, a factor likely to be particularly important on natural terrains. Again it will be instructive to look at the performance of wheelchairs. A standard wheelchair has 61 or 66 cm diameter driving wheels and 18 or 20 cm diameter casters (Kamenetz 1969). Although the fixed turning radius is 47 cm for a standard wheelchair, the average turning space required for a 180° turn is about 150 × 150 cm (Mohler and Sirkis 1972). The width of a standard wheelchair is 64 cm; a corridor about 150 cm wide is considered minimal for two people in wheelchairs to pass each other (Mohler and Sirkis 1972). By this criterion, the minimum space between obstacles to allow such a vehicle to pass would thus be about 75 cm. A human unencumbered by a wheelchair can, of course, do much better: One can pivot on one foot in the space of a decimeter, pass through a 30-cm space barely breaking stride, and ignore the spacing between low obstacles because one can simply step over them.

The absolute agility of a wheeled vehicle is a complex function of the number, placement, and size of the wheels and the width and length of the wheelbase. A direct and objective comparison between the agility of wheeled vehicles and legs is difficult, but an observation by Bulliet (1975) is relevant here. Commenting on the "oriental" plan and topography of cities where the camel has been the traditional form of transportation, Bulliet (1975) observes "Whoever has attempted to characterize medieval Middle Eastern and North African cities has sooner or later commented upon the narrow streets, the blind corners, the encroachment of buildings upon the public way, and in general upon the labyrinthine quality that strikes so forcibly the Western visitor. Many scholars have attributed this quality in some way to the Islamic religion and have implied that it is a universal feature of Islamic cities. None has seen it as a characteristic of a society without wheels (p. 224) . . . Wheeled vehicles—and this can come as no surprise to today's city dwellers—are inflexible in the restraints they put on city life. Streets must be flat, without stairsteps or precipitous grades, and, if possible, paved. Moreover, they must be maintained in this state if circulation is not to be interrupted. They must always be as wide as a single axle—as wide as two if the citizens are to be spared immoderate language. Corners must not be too sharp or narrow to be maneuvered; dead ends must be eschewed" (p. 226).

The maneuverability of wheeled vehicles is less than that of animals with legs; western culture's reliance on the wheels has determined the range of acceptable city plans. The lower maneuverability of the wheel would be a severe obstacle to its use by organisms on cluttered terrain, and a wheeled form of locomotion would be at a severe disadvantage on terrain encumbered with trees—one of the reasons for the necessity of trails and roads in settling the heavily forested eastern United States (Meyer 1917). For small or light vehicles, this limitation would extend to terrain bearing bushes and, for very small vehicles, even grass blades.

Appropriate habitats for wheeled organisms: theory and observations.—These factors may be used to circumscribe the types of natural terrains appropriate for wheelborne organisms, and to estimate the approximate sizes of such organisms. By focusing one's attention on particular habitats and dimensions of organisms, it is possible to identify at least one group of organisms in addition to bacteria that uses the principle of the rotating wheel for transportation; taking some liberties with the idea of a "wheeled organism," a second group may also be identified.

Wheels are an appropriate form of locomotion only on the Earth's surface; arboreal or fossorial wheeled organisms may be summarily eliminated from consideration. Highly dissected, precipitous terrain such as rocky mountainsides may also be eliminated, thus restricting our analysis to relatively flat terrain. Millimeter-sized wheels have been previously ruled out on the basis of the extreme irregularity of natural terrains at such a scale. Centimeter-sized wheels (and wheeled organisms) in forested or grassy habitats would face the problems of surmounting common obstacles (grass blades and clumps, branches) comparable in size to themselves and of negotiating spaces between obstacles small in relation to their bodies. Centimeter-sized wheels might be able to function, however, on dry, hard-packed soils where vegetation was sparse and the accumulation of vegetable debris was prevented. Such wheels would also be feasible on more compliant soils if wheel-loading were low; again, vegetation and detritus must be sparse. Do organisms with centimeter-sized wheels exist in such habitats?

If one is allowed a little license with the concept of a "wheeled organism," one such organism does exist, the dung beetle. East African savannahs are typified by dry, hard packed soils and sparse tufts of grass; plant detritus is quickly removed by the ubiquitous termites. In this habitat, dung beetles (*Scarabeus laevistriatus, S. catenatus, Kheper aegyptiorum, K. platynotus,* and *Gymnopleurus laevicollis*) form and roll balls of dung (a food provision for themselves or their larvae) which, depending on the species, may vary in diameter from about half a centimeter to about 5 cm (masses from about 7 g to about 250 g; Bartholomew and Heinrich 1978). The masses of the dung balls may exceed the masses of the beetles by over an order of magnitude, yet they are rolled distances of 1 to over 10 m at speeds of up to 20 cm/s (Bartholomew and Heinrich 1978).

Halffter and Matthews (1966), in a general review of the subfamily Scarabaeinae, note that "In the Palaearctic Region most, if not all, Scarabaeinae are found in prairie, steppe, and grassland-desert ecotones" (p. 59) while "in Africa Scarabaeinae predominate in the savanna. The forest-inhabiting species are few, and, in the case of the gallery forests which cross the savanna, most of the species inhabiting them are eurytopic" (p. 61). Halffter and Matthews (1966) also explicitly appreciated the importance of cluttered terrain in wheeled transport, stating that "the rolling behavior of the Scarabaeini . . . cannot be understood except in terms of an open environment, with few roots and leaf litter . . ." (p. 59). Although the principle of the wheel is used here to transport not the animal itself but a limiting resource for the animal, the point of interest is that the terrain involved has precisely the characteristics predicted to be permissive for wheeled transport (see Bartholomew and Heinrich [1978, fig. 8] and Heinrich and Bartholomew

[1979, p. 149] for photographs). In light of the previous discussion on the interaction of substrate irregularities and wheel diameter, it is also of interest to note that the smallest reported diameter for the dung ball of a dung beetle (*Boreocanthon probus*) is 4 mm (Halffter and Matthews 1966).

Decimeter- to meter-sized wheels are even easier to analyze, since this is a scale comparable to the wheels on wheelchairs, bicycles, and automobiles. Such wheels are of little utility on most natural terrains; extensive broken ground or fallen or close-set obstacles such as trees rule out their use. Given the high cost of transport of wheeled vehicles on compliant substrate, wheels are probably also energetically inferior to legs. Such wheels are limited to level open terrain such as savannah, grasslands, or deserts (as Gambaryan [1974] found while trying to pursue animals in the wild with automobiles and motorcycles). Wheels of these dimensions are, of course, used for transportation by one animal (*Homo sapiens*) on prepared terrain (roads and sidewalks, occasionally, parking lots), but this is a case more closely allied to the dung beetle than to strictly defined "wheeled organisms."

There is, however, one large and diverse group of organisms of these dimensions that uses the principles of the wheel for transportation, the broad variety of plants collectively known as tumbleweeds. Ridley (1930, p. 33) defines tumbleweeds as plants "in which the whole infructescence, or a part of the plant, or the whole of it carrying the seed, is torn off by the wind and drifted along, releasing and distributing the seed as it goes." Interestingly, Ridley (1930, p. 33) further comments that "This kind of dispersal is peculiar to deserts, steppes or prairies," while van der Pijl (1969, p. 58) claims that "In windswept steppe regions tumbleweeds are frequent, and travellers there have described how their dwellings were overrun by masses of rolling plant material." Fernald (1950) lists habitats for tumbleweeds as sandy shores and cultivated fields (*Salsola kali*), sandy soil (*Cycloloma atriplicifolium, Panicum capillare*), or dry prairies (*Psoralea argophylla*). Note that these habitats are again precisely those we have identified as being permissive for wheeled transport, flat ground without close-set bushes or trees. As was pointed out to me by J. Teeri, given that tumbleweeds tumble to disperse their seeds, they do so during the local dry season when aboveground vegetation such as grasses is minimal. One of the smaller of the tumbleweeds, *Spinifex squarrosus,* is 20–30 cm in diameter and is most common on sandy shores in the Indo-Pacific (Ridley 1930; also see van der Pijl 1969, fig. 16); obstacles to rolling will be minimal in this habitat. *Cycloloma atriplicifolium* and *C. platyphyllum*, common on the American plains, can exceed a meter in diameter. Ridley (1930) lists over 50 species of plants dispersed in this fashion; his presentation (pp. 32–38) supports many of the theoretical points made above and demonstrates that, in every situation in which environment allows wheeled transport to be useful, tumbleweeds have independently evolved.

Tumbleweeds circumvent both the high cost of rolling locomotion on compliant surfaces and the problems of surmounting obstacles by (1) their very low mass and high bearing surface, and (2) their exploitation of the wind velocity gradient near the ground (Vogel 1981) as an external, metabolically free source of power. Note that the traditional explanation for the rarity of rotating systems in nature, the difficulty in supplying nutrients through a rotating joint, does not apply here. In tumbleweeds, this problem is circumvented by (1) eliminating the rotating joint, and (2) being metabolically inactive during locomotion. The latter technique is a particularly clever way of circumventing the problems of supplying nutrients; remember that locomotion of tumbleweeds occurs for seed dispersal, and the only living portion of the plant during locomotion is the seeds themselves. This design, in which the entire external surface of the vehicle is the bearing surface of the wheel, has been used at least once in human technology as the design for a steam tractor (Spence 1960).

DISCUSSION

Biological wheels.—Bacterial flagella, dung beetles, and tumbleweeds all use rotating systems for locomotion. Other examples can also be offered, such as rolling spiders and caterpiller-tred stomatopods (Caldwell 1979), and the use of rolling as an escape behavior by pangolins (Tenaza 1975). The usual explanation for the lack of rotating systems in nature—the difficulty of supplying nutrients through a rotating joint—is probably valid and is supported by the present analysis. Bacteria circumvent this problem by being small enough that diffusion is sufficient to supply needed materials, which obviates the necessity of bulk transport across a rotating joint. Dung beetles and tumbleweeds avoid the problem by rotating only nonliving portions of the system. Note also that dung beetles and tumbleweeds minimize one of the limitations on wheeled transport, the difficulty in negotiating vertical obstacles. As stated above, no wheeled vehicle which depends on friction with the ground for driving force can surmount a vertical obstacle higher than its own radius. For both tumbleweeds and the dung balls of dung beetles, the driving force (the wind velocity gradient and the dung beetle, respectively) is external to the rotating system, and this limitation does not apply.

Constraints on the evolutionary process (Where the arguments went wrong).—The wheel is a symbol of progress and efficiency in Western cultures, and this cultural bias has determined the kinds of arguments presented in previous discussions of why organisms do not have wheels. If it is assumed that the wheel is the ideal mode of transport, then the dearth of wheels in biology must be explained by some intrinsic limitation on biological systems (see Lauder 1981; 1982). The wheel is indeed flawed as a mode of transport, and most animals would be far worse off if they used wheels for locomotion. The limitations which inhibit the evolution of wheeled transport in biological systems are primarily extrinsic to biology, lying instead in the mechanics of wheels. The natural environments in which wheels are even a feasible mode of transport are quite limited, but wherever rotating systems are useful, organisms have evolved to use them.

There are constraints on the evolution of wheels which are intrinsic to biological systems, but the biological constraints usually cited in these discussions do not seem to be the most important ones. Certainly there are structural problems involved in creating a rotating joint and supplying nutrients across such a joint, but organisms can circumvent such constraints by eliminating the rotating joint as tumbleweeds and dung beetles have done.

One truly intrinsic constraint on the evolution of rotating systems is the fact that the generation of mechanical forces in biological systems is almost universally based on the shearing and interdigitation of actin and myosin filaments. Were the rotating motor of prokaryotes more common in eukaryotes, fish with propellers might have arisen, but given the organization of eukaryote muscle, the generation of bending forces is more straightforwardly evolved and leads naturally to the evolution of oscillating flexible foils for thrust generation. While this may be considered an intrinsic biological constraint, one cannot fault organisms for never evolving systems which have structural demands at odds with preexisting morphology and which are energetically less efficient than more easily evolved systems.

There is a second constraint on the evolution of rotating systems which is restricted to terrestrial systems and which seems to me to be a constraint truly intrinsic to biology—the scaling limitations on wheeled transport. As has been shown above, wheeled transport does not scale well to small sizes since wheels become increasingly sensitive to the effects of substrate compliance and surface irregularities as size decreases. This implies that wheeled transport is likely to be useful only to relatively large organisms, organisms which are likely to be evolutionarily committed to a particular *Bauplan* and unable to evolve viable intermediate morphologies between their *Bauplan* and a wheeled organization. Only in cases in which the acquisition of wheeled transport arises from behavioral modifications, as in dung beetles and humans, or when the pre-existing morphology accidentally approximates a wheel, as in tumbleweeds, will wheeled transport evolve. This scaling limitation is a limitation truly intrinsic to biological systems and is probably a prime determinant of the scarcity of wheels in those few environmental settings where wheeled transport is feasible.

As I hope I have shown, in evaluating the significance of the particular morphologies evolved by organisms out of the set of conceivable morphologies, it is vital that one establish the physical and mechanical factors which affect the feasibility and utility of morphologies not shown by organisms. An assumption of imperfection in organisms is just as intellectually stifling a dogma as an assumption of the inherent perfection of organisms. Only by a careful analysis of function can one understand the significance of forms evolved and not evolved, and such an analysis, by focusing one's attention, may reveal aspects of the problem and examples of solutions previously overlooked.

SUMMARY

The scarcity of rotating systems in nature is a function primarily of the limited utility of such systems in natural environments; constraints intrinsic to biological systems (such as physiological problems of nutrient supply) are of secondary importance. In aquatic environments, rotating systems are advantageous only at low Reynolds numbers; in terrestrial environments, rotating systems are feasible as a form of transportation only on relatively flat, open terrain and become less useful as the size of the rotating element decreases. Prokaryotic flagella are popularly believed to be the only rotating system in nature, but dung beetles and

tumbleweeds also use such systems for transportation. Whenever rotating systems are a feasible mode of transportation, organisms have evolved that use these systems.

ACKNOWLEDGMENTS

I am grateful to G. Lauder, R. E. Lombard, L. Radinsky, R. R. Strathmann, S. Vogel, and R. Wassersug for helpful comments on this manuscript during various stages of its evolution. I am particularly indebted to J. Teeri for his help in researching tumbleweeds, to G. Lauder for crystallizing the concepts of intrinsic and extrinsic limitations, and to Eric Lombard for egging me on.

LITERATURE CITED

Adler, J. 1976. Introductory remarks: Some aspects of the structure and function of bacterial flagella. Pages 29–34 *in* R. Goldman, T. Polland, and J. Rosenbaum, eds. Cell motility. Book A. Motility, muscle and non-muscle cells. Cold Spring Harbor Conf. on Cell Proliferation. Vol. 3. Cold Spring Harbor Laboratory, N.Y.

Anonymous, 1975. Technical handbook for facilities engineering and construction manual. Part 4. Facilities design and construction. U.S. Dep. Health Educ. Welfare, Tech. Handb. Ser.

Barnes, R. D. 1974. Invertebrate zoology. Saunders, Philadelphia, Pa.

Bartholomew, G. A., and B. Heinrich. 1978. Endothermy in African dung beetles during flight, ball making, and ball rolling. J. Exp. Biol. 73:65–83.

Bekker, M. G. 1956. Theory of land locomotion. University of Michigan Press, Ann Arbor, Mich.

Bulliet, R. W. 1975. The camel and the wheel. Harvard University Press, Cambridge, Mass.

Burdett, R. G., B. A. Cohen, C. Gonella, G. W. Kelly, and A. F. Morris. 1977. Emory detachable motor drive for the standard wheelchair. Arch. Phys. Med. Rehabil. 58:328–331.

Caldwell, R. L. 1979. A unique form of locomotion in a stomatopod—backward somersaulting. Nature 282:71–73.

Denny, M. W. 1981. A quantitative model for the adhesive locomotion of the terrestrial slug, *Ariolimax columbianus*. J. Exp. Biol. 91:195–217.

Denny, M. W., and J. M. Gosline. 1980. The physical properties of the pedal mucus of the terrestrial slug, *Ariolimax columbianus*. J. Exp. Biol. 88:375–393.

Fernald, M. L. 1950. Manual of botany. American Book Co., New York.

Gambaryan, P. P. 1974. How mammals run. Wiley, New York.

Gould, S. J. 1981. Kingdoms without wheels. Nat. Hist. 90:42–48.

Halffter, G., and E. G. Matthews. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entomol. Mex. 12-14; 1–312.

Heinrich, B., and G. A. Bartholomew. 1979. The ecology of the African dung beetle. Sci. Am. 241:146–156.

Herreid, C. F., D. A. Prawel, and R. J. Full. 1981. Energetics of running cockroaches. Science 212:331–332.

Hilmen, M., and M. Simon. 1976. Motility and the structure of bacterial flagella. Pages 35–46 *in* R. Goldman, T. Pollard, and J. Rosenbaum, eds. Cell motility. Book A. Motility, muscle and non-muscle cells. Cold Spring Harbor Conf. on Cell Proliferation. Vol. 3. Cold Spring Harbor Laboratory, N.Y.

Holberton, D. V. 1977. Locomotion of Protozoa and single cells. Pages 279–332 *in* R. McN. Alexander and G. Goldspink, eds. Mechanics and energetics of animal locomotion. Wiley, New York.

Holwill, M. E. J. 1977. Low Reynolds number undulatory propulsion in organisms of different sizes. Pages 233–242 *in* T. J. Pedley, ed. Scale effects in animal locomotion. Academic Press, New York.

Jones, H. D. 1978. Fluid skeletons in aquatic and terrestrial animals. Pages 267–281 *in* K. Schmidt-Nielsen, L. Bolis, and S. H. P. Maddrell, eds. Comparative physiology: water, ions, and fluid mechanics. Cambridge University Press, Cambridge.

Kamenetz, H. L. 1969. The wheelchair book. Charles C. Thomas, Springfield, Ill.

Katz, J., and D. Weihs. 1978. Hydrodynamic propulsion by large amplitude oscillation of an airfoil with chordwise flexibility. J. Fluid Mech. 88:485–497.

———. 1979. Large amplitude unsteady motion of a flexible slender propulsor. J. Fluid Mech. 90:713–723.

Larrabee, E. E. 1980. The screw propeller. Sci. Am. 243:134–148.

Lauder, G. V. 1981. Form and function: structural analysis in evolutionary morphology. Paleobiology 7:430–442.

———. 1982. Historical biology and the problem of design. J. Theor. Biol. 97:57–67.

Meyer, B. H. 1917. History of transportation in the United States before 1860. Carnegie Institution of Washington, Washington, D.C.

Miller, V. P. 1973. Accommodations for the physically handicapped. Veterans Administration Construction Standard CD-28, October 15, 1973.

Mohler, S. R., and J. A. Sirkis. 1972. Airport medical design guide. Aerospace Med. 43:903–911.

Peizer, E., D. Wright, and H. Freiberger. 1964. Bioengineering methods of wheelchair evaluation. Bull. Prosthet. Res. 10:77–100.

Purcell, E. M. 1977. Life at low Reynolds number. Am. J. Physics 45:3–11.

Ridley, H. N. 1930. The dispersal of plants throughout the world. L. Reeve, Ashford, Kent, England.

Rouse, H. 1946. Elementary mechanics of fluids. Dover, New York.

Scherer, J. O. 1968. Experimental and theoretical investigations of large amplitude oscillating foil propulsion systems. Hydronautics Inc. Tech. Rep. no. 662-1.

Silverman, M., and M. Simon. 1974. Flagellar rotation and the mechanism of bacterial motility. Nature 249:73–74.

Sleigh, M. A. 1978. Fluid propulsion by cilia and flagella. Pages 255–266 *in* K. Schmidt-Nielsen, L. Bolis, and S. H. P. Maddrell, eds. Comparative physiology: water, ions, and fluid mechanics. Cambridge University Press, Cambridge.

Spence, C. G. 1960. God speed the plow. The coming of steam cultivation to Great Britain. University of Illinois Press, Urbana, Ill.

Streeter, V. L. 1966. Fluid mechanics. McGraw-Hill, New York.

Tenaza, R. R. 1975. Pangolins rolling away from predation risks. J. Mammal. 56:275.

Trueman, E. R. 1975. The locomotion of soft-bodied animals. American Elsevier, New York.

van der Pijl, L. 1969. Principles of dispersal in higher plants. Springer-Verlag, New York.

Vogel, S. 1981. Life in moving fluids. Duxbury, North Scituate, Mass.

Voight, E. D., and D. Bahn. 1969. Metabolism and pulse rate in physically handicapped when propelling a wheel chair up an incline. Scand. J. Rehabil. Med. 1:101–106.

Webb, P. W. 1977. Effects of size on performance and energetics of fish. Pages 315–332 *in* T. J. Pedley, ed. Scale effects in animal locomotion. Academic Press, New York.

Went, F. W. 1968. The size of man. Am. Sci. 56:400–413.

Wilson, S. S. 1973. Bicycle technology. Sci. Am. 228:81–91.

Wolfe, G. A., R. Walters, and H. J. Hislop. 1977. Influence of floor surface on the energy cost of wheelchair propulsion. Phys. Ther. 57:1022–1027.

Wong, J. Y. 1978. Theory of ground vehicles. Wiley, New York.

Wu, T. Y. 1977. Introduction to the scaling of aquatic animal locomotion. Pages 203–232 *in* T. J. Pedley, ed. Scale effects in animal locomotion. Academic Press, New York.