# Molecules, muscles, and machines: Universal performance characteristics of motors

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Animal- and human-made motors vary widely in size and shape, are constructed of vastly different materials, use different mechanisms, and produce an enormous range of mass-specific power. Despite these differences, there is remarkable consistency in the maximum net force produced by broad classes of animal- and human-made motors. Motors that use force production to accomplish steady translational motion of a load (myosin, kinesin, dynein, and RNA polymerase molecules, muscle cells, whole muscles, winches, linear actuators, and rockets) have maximal force outputs that scale as the two-thirds power of mass, i.e., with cross-sectional area. Motors that use cyclical motion to generate force and are more subject to multiaxial stress and vibration have maximal force outputs that scale as a single isometric function of motor mass with mass-specific net force output averaging 57 N·kg<sup>-1</sup> (SD = 14). Examples of this class of motors includes flying birds, bats, and insects, swimming fish, various taxa of running animals, piston engines, electric motors, and all types of jets. Dependence of force production and stress resistance on cross-sectional area is well known, but the isometric scaling and common upper limit of mass-specific force production by cyclical motion motors has not been recognized previously and is not explained by an existing body of theory. Remarkably, this finding indicates that most of the motors used by humans and animals for transportation have a common upper limit of mass-specific net force output that is independent of materials and mechanisms.

Organisms and machines move by exerting forces on their external environment, and the upper limit of force output affects performance variables such as acceleration and maximum load. The product of force and velocity is power, and motor performance often is thought of in terms of power output rather than force output. Here we concentrate strictly on force output to reveal universal characteristics of motors that are obscured by differences in power.

Force output is accomplished by a specialized structure (a motor), the mass of which generally constitutes a significant portion of the total device mass. The amount of force that a motor produces in relation to its mass (specific force) affects material costs for construction, energy efficiency, and the amount of payload that can be transported. Other criteria such as procurement costs, fuel consumption, maximum speed, noise, and emissions certainly affect design and selection of a motor for a given application (1); however, one theoretical ideal is a very small motor that produces a very high force. This ideal is particularly apparent in applications such as flight, where weight is critical. Improving motor "thrust-to-weight" ratio is an ongoing quest for designers of aircraft engines  $(1, \dagger)$  and presumably is a target of natural selection in flying animals, which show tradeoffs between the size of the flight motor and important payload such as ovaries (2). Thus, both human design and organic evolution are attempting continually to make motors that produce higher specific force.

Increasing the specific force output of a motor requires lighter materials, greater stresses on component parts, and/or more optimized mechanics. Engineers and biologists have devoted considerable effort to studying the stresses experienced within the materials and component parts of motors (e.g., refs. 1 and 3–5, †), with engineers looking for ways to improve durability and/or performance and biologists seeking to understand the function and evolution of natural design. For both animate and inanimate motors, these efforts have included dimensional analyses of the scaling of stresses within motor components  $(4, 5, \ddagger)$ , but there has been little effort to examine the scaling trends of net force output. One notable exception is a wide-ranging review of the maximum forces generated by animals (6), but that study contains a mixture of peak instantaneous and time-averaged forces, and it addresses the scaling of forces in relation to body mass rather than to motor mass (the latter is true also for a more narrowly focused study of forces generated by beetles (7). As a result, neither engineers nor biologists have a well formed view of how net force output varies according to motor mass. Here we perform such an analysis and demonstrate striking similarities in the mass scaling and magnitude of force output for broad classes of motors.

# Methods

We accumulated data for the maximal net force output and motor mass of a wide variety of animal- and human-made devices. We sought a sample that is representative of the widest range of sizes and design varieties including the most modern and high-performance motors. In cases where the time course of force output was reported (i.e., traces of instantaneous forces), we have taken the time-averaged force over a single complete cycle. Our data set includes the following.

## Force Outputs by Animate Motors.

- 1. Forces generated by single myosin (8), kinesin (9), dynein (10), and RNA polymerase (11) molecules producing static tension.
- 2. Forces produced by molecular motors: a bacterial flagellar motor (12), the  $F_0F_1$ -ATPase ion pump (13), mammalian sperm, the flagellum of which beats with a helical wave motion (14), and the helical spasmoneme spring of the protozoan *Vorticella* (15).
- 3. Tension produced by muscle cells or whole muscles while maximally stimulated and clamped at constant length (refs. 16–24; all these measures are for the muscle only; forces are parallel to the axis of strain, and there are no external levers). This sample includes muscles of mollusks, insects, fish, frogs, and mammals.
- 4. Net force output by flying insects, birds, and bats as determined from the maximum load lifted during takeoff from the ground in still air (25–27). These data encompass a wide range of taxa, body forms, and flight styles.
- Mean ground reaction forces (resultant of vertical, fore-aft, and lateral force vectors in cases where all three were measured) from single or paired legs during running or hopping by cockroaches (28), iguanas (29), kangaroo rats

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<sup>&</sup>lt;sup>†</sup>Lord, W. K., MacMartin, D. G. & Tillman, T. G., Fluids 2000, June 19–22, 2000, Denver, CO. <sup>‡</sup>Epstein, A. H., Jacobson, S. A., Protz, J. M. & Frechette, L. G., 8th International Symposium on Transport Phenomena and Dynamics of Rotating Machinery (ISROMAC-8), March 26–30, 2000, Honolulu, HI.

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(30), and dogs (31), along with forces calculated from acceleration of the body center of mass for running humans (32).

6. Forces calculated from maximum whole-body acceleration during bursts of swimming by crayfish (33) and fish (34).

## Force Outputs by Inanimate Motors.

- 1. Maximal thrust at sea level by jet engines (see www.aircraftenginedesign.com, www.geae.com, and www.bairdtech.com/ bmt/BMT80.htm; these include data from thrust augmentation by afterburning in military jets).
- 2. Takeoff thrust of rockets (see www.bestofcolumbus.com/ Braeunig/space/specs.htm and www.thrustcurve.com; these include data from a mixture of solid and liquid fuel propulsion systems).
- Maximal force output of piston engines (ref. 35 and www.ferrari. com, www.honda-engines.com, www.lycoming.textron.com, www.hobby-lobby.com, www.hobbypeople.net/prodinfo/ magnum/magxl.htm, www.cummins.com, www.caterpillar. com, and www.manbw.dk). These measures were obtained by dividing maximum crankshaft torque by crankshaft radius (half of piston-stroke length), or if maximum torque was not reported we used data for maximum power, cycle frequency at maximum power, and crankshaft radius (power =  $2\pi$ -freq·torque). We have included from ref. 35 only motors of mass greater than 2 kg, because cycle frequency and net force output of smaller engines (model airplane applications) vary widely depending on the propeller that is used. The estimation of maximum thrust (i.e., at low forward speed) for a sample of contemporary small model airplane engines fitted with specific propellers was performed for us by Landing Products, the manufacturer of APC propellers (www. apcprop.com).
- 4. Maximum sustainable force output by linear and rotary electrical induction motors (see www.lineardrives.com/ technical\_specifications.htm, www.calinear.com, www.thrust-tube.com, www.powertecmotors.com, and www.hobby-lobby.com). These include data from an artificial human heart that is powered by a linear induction motor (36) and motors that use AC or DC power with or without brushes.
- Maximum force loads for both gas- and electric-powered winches and hoists (www.pacificwinches.com/pacwinches/ index.htm, www.winchcentral.com, and www.irhoist.com).
- 6. Maximum static thrust or tensile forces generated by linear actuators (www.racointernational.com and www.motionsystem. com) and materials testing machines (www.instron.com).
- 7. In addition to the sources listed above, we obtained force outputs for a piston engine and a jet engine that were produced recently by the National Aeronautics and Space Administration General Aviation Propulsion program (personal communication with L. A. Burkardt, National Aeronautics and Space Administration General Aviation Propulsion program manager, and K. Chatten, Senior Project Engineer, Teledyne), the goals of which included increasing the thrust-to-weight ratio of motors used for aviation. We also obtained data for two other recent experimental microturbine motors<sup>‡</sup> (www.m-dot.com) that are part of military research projects, the aims of which require minimizing motor size and weight. We highlight these to emphasize that our sample includes the most recent and sophisticated designs.

**Motor Mass.** Measures of motor mass for flying animals consist of the total mass of the flight musculature and wings. Motor mass for swimming fish is the total mass of myotome musculature used in swimming. Motor mass for running animals was not reported in the original studies, thus it is approximated here as 10% of body mass per leg except for cockroaches, for which we use the reported 2% of body mass per leg. Measures of motor mass for

machines are the mass of the motor exclusive of external support structures and fuel. Measures of motor mass for rockets are the sum of the rocket dry mass and propellant mass at takeoff (for rockets the motor is the fuel, which is why fuel mass is included here but not for other devices). The mass of single molecules was obtained by dividing molecular weight by Avagadro's number. The mass of molecular motors was calculated from the molecular weight and number of all component molecules ( $F_0F_1$ -ATPase) or from estimates based on motor dimensions and density. The mass of linear induction motors (LIMs) is variable, because they can be equipped with a thrust rod of any length. Aside from the LIM-driven artificial heart that has fixed dimensions, we calculated mass of LIMs by using a thrust-rod length that is twice the length of the stator, because the result would be about the minimum thrust-rod length to provide a generally useful range of motion.

## Results

Maximal force output of motors tends to scale either isometrically (mass<sup>1.0</sup>) or allometrically according to cross-sectional area (mass<sup>2/3</sup>). This tendency can be seen in Table 1, which identifies two major groups that show similar regression coefficients for the mass scaling of maximum force output. Group 1 consists of motors that use force production to accomplish steady translational motion of a load (single molecules, muscles, winches, linear actuators, and rockets). For Group 1 motors, one scaling equation [force = 887·mass<sup>0.667</sup> (units are N and kg);  $r^2 = 0.994$ ; Fig. 1] describes force output over a range of 27 orders of magnitude of motor mass from myosin molecules to the solid fuel booster rocket of the space shuttle.

A second group of motors is clearly distinguishable (Table 1) by scaling relationships in which force varies in a nearly isometric fashion with motor mass. These are the motors of flying birds, bats, and insects, swimming fish, running animals, piston engines, linear and rotary electric motors, and all types of jets. The distinguishing characteristic of these Group 2 motors is that they use repetitive or cyclical motion to generate nonsteady force and presumably are more subject to multiaxial stress and vibration (at a given specific force output) than the motors in Group 1. When we lump all the Group 2 motors together (Fig. 2), their maximal force output scales as a single isometric function of motor mass [55·mass<sup>0.999</sup> (units are N and kg);  $r^2 = 0.999$ ], with mass-specific net force output averaging 57 N·kg<sup>-1</sup> (SD = 14; see Fig. 2 *Inset*).

The only motors that do not adhere to these two general scaling trends are the small group of molecular motors (mammalian sperm, a bacterial flagellar motor, and the helical spasmoneme spring of *Vorticella*), which fall between the two lines in Figs. 1 and 2. The kinematics of these molecular motors feature large lateral motions and presumably a higher level of multiaxial stress than molecules such as myosin or kinesin that produce translational motion and scale with Group 1. This result suggests that small Reynold's numbers and force regimes dominated by viscosity rather than inertia can change the scaling of specific force output for motors that would otherwise be expected to scale with Group 2. This result also suggests that inertia is an important feature of whatever mechanical phenomena unite the mass-specific force outputs of Group 2 motors.

Although they produce surprisingly invariant-specific force outputs, Group 2 motors vary widely in their specific power outputs. Two grams of hummingbird flight muscle (37) produce  $\approx 0.65$  W, whereas the Massachusetts Institute of Technology microjet<sup>‡</sup> of the same mass produces  $\approx 10$  W. Because their specific force outputs do not vary, these differences in specific power come primarily from changes in the velocity of oscillating or rotating components (i.e., the 32-Hz oscillation frequency of 8-cm hummingbird wings versus the 20-kHz rotation frequency of the 1-cm microjet turbine). Making the comparison across a large size range reveals an even

Table 1. Fitting terms from least-squares linear	regressions of log <sub>10</sub> maximum	force output (N) as a function	of log <sub>10</sub> motor mass (kg)
for different types of motors			

Motor type	Intercept	Slope	<i>r</i> <sup>2</sup>	Ν	SE slope	Minimum mass	Maximum mass
Group 1							
Muscles	2.995	0.677	0.997	16	0.010	$4.8 imes10^{-22}$	0.014
Rockets	2.737	0.719	0.988	19	0.019	0.0079	$5.87 imes10^5$
Winches	3.251	0.736	0.852	6	0.154	14.5	1,361
Linear actuators	3.048	0.612	0.656	9	0.167	0.34	2,587
Mean	3.008	0.686					
Group 2							
Running animals	1.703	0.949	0.998	5	0.023	0.00004	32.7
Swimming animals	1.672	0.924	0.992	8	0.033	0.0009	0.04
Flying birds	1.555	0.959	0.993	11	0.026	0.002	0.37
Flying bats	1.862	1.082	0.994	7	0.037	0.002	0.013
Flying insects	1.583	0.959	0.982	149	0.011	$3.7 imes10^{-7}$	0.008
Turbines	1.811	0.963	0.993	21	0.018	0.002	4,264
Turbofans	1.793	0.986	0.934	30	0.049	64	6,804
Electric rotary motors	1.739	1.078	0.999	10	0.013	0.04	558
Linear induction motors	1.825	0.854	0.940	7	0.096	1.9	32.6
Piston engines	1.719	1.016	0.988	31	0.021	0.165	2,744
Mean	1.726	0.977					

The slope of these log-log regressions is *b* in the equation  $y = ax^b$ ; the inverse log of the intercept is *a*. *N* shows the sample size within each category of motor; SE is the standard error of the least-squares regression slope. Minimum and maximum motor masses (kg) are shown for each category. The data are separated into two groups that are distinguished by slope and intercept. Single molecules that create translational motion (myosin, kinesin, and dynein) are included here with muscle cells and whole muscles (treating muscles alone yields a nearly identical scaling equation). Piston engines greater than 4,400 kg mass are excluded, because they scale differently than smaller piston engines (see text and Fig. 3).

greater range of specific power output. The thoracic musculature and wings of a fruit fly (27) generate  $\approx 80 \text{ W} \cdot \text{kg}^{-1}$ , whereas jet engines can produce power outputs in excess of 10,000 W \cdot kg^{-1}. Consistent specific force output over an enormous range of specific



**Fig. 1.** Maximum net force output as a function of motor mass for translational motors (Group 1 motors). The solid line is the least-squares regression equation fit to the log-transformed data. This linear regression equation is  $\log_{10}$  force = 2.95 + 0.667  $\log_{10}$  mass (units are N and kg;  $r^2$  = 0.994; SE of the slope = 0.007). The dashed line is the isometric scaling equation for the Group 2 motors shown in Fig. 2. Molecular motors (circular symbols) were excluded from the regression fit; they operate in a viscous rather than an inertial regime and conform to neither of the two scaling equations that describe net force output of all other types of motors.

power clearly indicates that force production rather than power production is the limiting factor for motor performance across divergent types of motors. This is not to say that power output cannot be a limiting factor within specific types of motors or is generally unimportant, for on the contrary, power output has much to do with speed, economy, noise, emissions, heat production, and so forth. Our point is simply that specific power output varies much more so than does specific force output.

An interesting feature of the two distinct scaling relationships shown in Figs. 1 and 2 is that they intersect at a mass of  $\approx$ 4,400 kg. If the force output of Group 2 motors were to continue to increase isometrically at motor masses greater than 4,400 kg, they would need to produce more force per cross-sectional area than do Group 1 motors. This seems unlikely, because the force output of Group 1 motors presumably is limited by an upper bound of uniaxial stress. Thus, the scaling of force production by Group 2 motors should change from isometric to allometric at motor masses greater than 4,400 kg. We tested this prediction by examining data for piston engines that were not included in Fig. 1 and thus are independent of our scaling equations. Fig. 3a shows net force output as a function of mass for piston engines ranging in size from 0.17 to 1,901,000 kg (model airplanes to oil tankers). The isometric equation for Group 2 motors fits precisely the sample of piston engines less than 4,400 kg, whereas the allometric equation for Group 1 motors fits the upper bound of force output for piston engines greater than 4,400 kg. Analysis of covariance shows that separate regression lines fit to these data for motors above and below 4,400 kg have significantly different slopes (P < 0.0001). This inflection point at 4,400 kg is even more pronounced for geometric data (Fig. 3b). A tight relationship that describes the mass scaling of the ratio of total piston cross-sectional area to stroke length (chosen because this index captures two geometric variables) across 4 orders of magnitude, up to a mass of 4,400 kg, does not apply for larger engines, which show a great diversification in their design. Because the scaling relationships in Figs. 1 and 2 were not known previously, it is likely that this sharp transition in piston engine geometry is primarily the outcome of trial and error rather than



**Fig. 2.** Maximum net force output as a function of motor mass for Group 2 motors. The solid line is the least-squares regression equation fit to the log-transformed data. This linear regression equation is  $\log_{10}$  force = 1.74 + 0.999  $\log_{10}$  mass (units are N and kg;  $r^2$  = 0.999; SE of the slope = 0.002). The dashed line is the allometric scaling equation for translational Group 1 motors shown in Fig. 1. (*Inset*) Frequency distribution of specific force outputs for all Group 2 motors.

an understanding that there is a fundamental change in factors that limit engine performance above and below a certain mass.

### Discussion

Allometric scaling of force output according to cross-sectional area (mass<sup>2/3</sup>) is an expected result for Group 1 motors. These motors are built to move loads in a translational fashion in such a way that stresses are developed gradually and predictably, with maximum force output occurring at or near the static breaking

stress of critically loaded parts. More surprising is the similarity of the intercepts of the Group 1 scaling equations (Table 1) and the adherence of all Group 1 motors to a single scaling equation (Fig. 1) rather than a series of parallel equations. Mass-specific ability of materials to resist static uniaxial stress is given by the ratio of elastic modulus to density (3), which increases by a factor of 16 between muscle and steel, yet the ratio of the scaling constants for muscles versus machines (reverse-transformed intercepts from Table 1) is close to unity. Thus, regression



**Fig. 3.** (*A*) Maximum net force output as a function of motor mass for piston engines. Older engines are represented by open symbols (many date from the 1930s and 1940s; ref. 35); contemporary piston engines are represented by solid symbols. The solid line is the scaling equation derived from the data in Fig. 2; the dashed line is the scaling equation derived from the data in Fig. 1. (*B*) The relationship between motor mass and the ratio of piston total cross-sectional area to piston stroke length. The solid line is the least-squares regression equation fit to the log-transformed data for motors less than 4,400 kg in mass ( $log_{10}$  piston area/stroke length =  $-160 + 0.617 log_{10}$  mass; units are m and kg).

equations describing the mass dependence of force output of these devices are much more similar than would be expected based on static material properties.

Log-log plots tend to deemphasize important variation, and that is certainly the case for the Group 1 motors in our sample. The average absolute deviation from the regression line in Fig. 1 is 0.28 log units, and the data tend to fall within a band that is  $\approx 1$  logarithmic unit in height (i.e., force output of Group 1 motors at a given mass can vary by as much as a 10:1 ratio). These differences undoubtedly are functionally significant.

Force outputs of Group 2 motors are considerably less variable than Group 1 (average absolute deviation from the regression line in Fig. 2 is 0.07 log units), and their conformance to a single isometric scaling relationship (Fig. 2 and Table 1) cannot be explained readily. All the devices in this group use rotary or oscillatory motion with cycle frequencies that scale inversely with length (i.e., as  $l^{-1}$  or mass<sup>-1/3</sup>). Accordingly, dimensional analysis for the mass scaling of force output (using  $F = \max r\alpha$ , where r is the rotor radius, and  $\alpha$  is the angular acceleration) predicts that force should be proportional to  $l^3 \tilde{l}^1 l^{-2}$ , which would result in force output scaling with length<sup>2</sup> or mass<sup>2/3</sup>, just as occurs in Group 1 motors. Engineers have emphasized the desirability of maintaining system dynamic performance (i.e., dynamic similarity) when designing differently sized devices such as robots.§ This design constraint entails invariant accelerations for equivalent structural elements and therefore forces that scale with mass rather than area. Likewise, the limbs of running animals have been shown to be similar dynamically (38). Thus, isometric scaling of force output of Group 2 motors is in agreement with the principle of dynamic similarity, but that is hardly a satisfying result, because it leaves unanswered the question of why one scaling equation describes all Group 2 motors (Fig. 2) rather than a series of parallel equations with different elevations or why the variation around the Group 2 scaling equation is less than the variation seen in Group 1 motors. It also fails to explain why a motor such as the Massachusetts Institute of Technology mircrojet<sup>‡</sup> that was designed *de novo* using materials and mechanisms different from any previous turbine generates a specific force of 55 N·kg<sup>-1</sup>, which is almost exactly the mean value for all other animate and inanimate Group 2 motors. What enforces such strict adherence to maximum force output in the neighborhood of  $\approx 60 \text{ N} \cdot \text{kg}^{-1}$  for devices and organisms that seem so fundamentally different? This is a question that we cannot answer. Perhaps there is a simple explanation that we have overlooked, or perhaps it will become another example (39) of scale invariance and universality that resists mechanistic explanation.

An interesting aspect of the two different scaling relationships is that some of the motors in one group are components of motors in the other group. For example, winch motors are included in our sample of electrical motors, the force output of which scales isometrically with mass, yet the force output of whole winches scales allometrically with other Group 1 motors that move loads in a steady translational fashion. A reverse example is that of muscles and animal motors. Individual myosin molecules, muscle cells, and individual muscles have force outputs that scale allometrically (Group 1), yet they are major components of the animal motor systems, the force outputs of which scale isometrically (Group 2). In both winches and animal limbs there are lever systems that either increase force at the cost of speed (winches) or increase speed at the cost of force (animal limbs). Apparently, lever systems that produce steady translational motion can produce forces that are limited ultimately by a critical cross-sectional area, whereas lever systems involved in more complex motion and time-varying forces are constrained to producing forces that scale isometrically with mass. These results suggest that there are as yet poorly understood relationships between stress regimes and device mass that unite the

mass-specific performance of motors in ways that are not affected greatly by higher-level variables (i.e., materials and mechanisms) other than the ability to switch between allometric versus isometric scaling depending on the complexity of the stress regime.

One mechanism that changes allometric scaling of muscle force to isometric scaling of whole-motor force in animal lever systems has to do with departures from geometric similarity and the allometric scaling of mechanical advantage. For any lever, the product of force and length on one side of the fulcrum is equal to the product of force and length on the other side of the fulcrum. Thus, the ratio of muscle force to whole-limb force is equal to the ratio of the lever-arm lengths between the muscle and the joint and between the joint and the end of the limb. Ratios of lever arms (mechanical advantage) in the legs of mammals have been shown to scale allometrically. One result of this departure from geometric similarity is that peak stresses in bones, muscles, and tendons are mass-independent across wide ranges of animal size (4, 5). This result has been interpreted as a design constraint that is necessary to accommodate the different scaling of body weight and crosssectional area. Although this argument remains valid, the data presented here suggest that the story is more general, because isometric scaling of mass-specific force output occurs in fish, the locomotor apparatus of which does not support body weight. There seems to be a more fundamental reason why motor geometry needs to be arranged to conserve mass-specific force output per se without reference to weight or conservation of stress.

A consequence of the allometric scaling of force output by motors exceeding 4,400 kg (Fig. 3) is that they start to become restricted in the types of functions that they are suitable to perform. The very large motors used to power trains and ships and to generate electricity have specific force outputs that render them unsuitable for applications that are particularly weightsensitive. For example, the Burmeister and Wain K98MC-C engine (mass = 1,900,000 kg) used to propel oil tankers produces a specific force output of less than 3 N·kg<sup>-1</sup>. The largest jet engines (6,800 and 4,200 kg used on Boeing 777 and 747 jets, respectively) and the largest piston engine ever built for aircraft (the 2,700-kg Lycoming XR-7755) are near or slightly above the size at which specific force of Group 2 motors begins to scale allometrically rather than isometrically. Based on these data, it seems that aircraft engines show little potential for size increases substantially beyond the largest engines that exist already. For applications involving very large aircraft, the use of multiple engines at or below the size of the largest extant engines should be more viable than attempting to build larger engines.

The results of our study point out the need for an improved theoretical understanding of the principles that impose mechanism- and material-independent limits on the specific force output of motors. Improved knowledge in this area may not make it possible to extend the present upper bound of specific force (keep in mind that animals and evolution have been unable to do so), but it would at least sharpen our view of what is attainable. As an example of how such knowledge would be helpful, consider the field of aerospace engineering, in which there is a general lack of consensus regarding the recent progress, future, or scalability of thrust-to-weight ratios for jets. Designers of the Massachusetts Institute of Technology microjet (40) predicted that "a millimeter-size engine would have a thrust-to-weight ratio of about 100:1, compared with 10:1 for the best modern aircraft engines." As discussed above, it has turned out that their microjet produces a 5.5:1 thrust-to-weight ratio (thrust to mass = 55  $N \cdot kg^{-1}$ ). A prominent text (see page 357 of ref. 1) states that thrust-to-weight ratios of jets have been improving steadily since 1965 and "are expected to continue for some time," whereas a recent review<sup>†</sup> that plots the maximum thrust-to-weight ratios of jets introduced since 1955 shows that this metric has remained nearly constant since 1970 and concludes that "it is clear that we are approaching a limit in our

<sup>&</sup>lt;sup>§</sup>Pollard, N. S. & Hodgins, J. K., Yale Workshop on Adaptive and Learning Systems, June 10–12, 1998.

ability to improve performance with existing technology." The next generation of U.S. fighter jet engine, the F119, presently under development by Pratt & Whitney, has a goal of achieving a specific thrust of 100 N·kg<sup>-1</sup> without using afterburners. This would place it within the upper tail of the distribution of specific force for Group 2 motors (Fig. 2 Inset) and therefore presumably near a universal failure mode. The turbine of a prototype F119 failed during a test fire and was subsequently redesigned, making it 68 kg more massive (personal communication from Lt. Col. A. K. Mitchell, U.S. Air Force). Both the mass and realized thrust of this engine remain classified. As this engine evolves and accumulates a record of field service, it will be interesting to see whether it can attain its target thrust-to-weight specification without making tradeoffs in areas such as durability. We highlight these examples to illustrate the lack of previous recognition of general scaling relationships and universal upper limits of motor force output, to show that the most current designs have not significantly exceeded the maximum force outputs indicated by our data set, and to establish the need for theoretical exploration.

- 1. Kerrebrock, J. L. (1992) Aircraft Engines and Gas Turbines (MIT Press, Cambridge, MA).
- 2. Marden, J. H. & Chai, P. (1991) Am. Nat. 138, 15-36.
- Ashby, M. F. (1999) Materials Selection in Mechanical Design (Butterworth-Heinemann, Oxford), 2nd Ed.
- 4. Biewener, A. A. (1989) Science 245, 45-48.
- Alexander, R. M., Jayes, A. S., Maloiy, G. M. O. & Wathuta, E. M. (1981) J. Zool. 194, 539–552.
- 6. Alexander, R. M. (1985) J. Exp. Biol. 115, 231-238.
- 7. Evans, M. E. G. & Forsythe, T. G. (1984) J. Zool. 202, 513-534.
- Finer, J. T., Simmons, R. M. & Spudich, J. A. (1994) Nature (London) 368, 113–119.
- Shingyoji, C., Higuchi, H., Yoshimura, M., Katayama, E. & Yanagida, T. (1998) Nature (London) 393, 711–714.
- 10. Schnitzer, M. J., Visscher, K. & Block, S. M. (2000) Nat. Cell Biol. 2, 718-723.
- Wang, M. D., Schnitzer, M. J., Yin, H., Landick, R., Gelles, J. & Block, S. M. (1998) Science 282, 902–907.
- 12. Berg, H. C. (1993) Random Walks in Biology (Princeton Univ. Press, Princeton).
- Sambongi, Y., Iko, Y., Tanabe, M., Omote, H., Iwamoto-Kihara, A., Ueda, I., Yanagida, T., Wada, Y. & Futai, M. (1999) *Science* 286, 1722–1724.
- Schmitz, K. A., Holcomb-Wygle, D. L., Oberski, D. J. & Lindemann, C. B. (2000) *Biophys. J.* 79, 468–478.
- 15. Mahadevan, L. & Matsudaira, P. (2000) Science 288, 95-100.
- 16. Marden, J. H. (1995) J. Exp. Biol. 198, 2087-2094.
- 17. Fitzhugh, G. H. & Marden, J. H. (1997) J. Exp. Biol. 200, 1473-1482.
- 18. Peters, S. E. & Aulner, D. A. (2000) J. Exp. Biol. 203, 3639-3654.
- 19. Ettema, G. J. (1996) J. Exp. Biol. 199, 1277-1285.
- 20. Olson, J. M. & Marsh, R. L. (1993) J. Exp. Biol. 176, 175-193.
- 21. Lou, F., Curtin, N. A. & Woledge, R. C. (1997) J. Exp. Biol. 200, 495-501.

Achieving a theoretical understanding of general factors that ultimately limit the ability of Group 2 motors to produce forces and withstand complex stress regimes is a considerable challenge that probably will require decades of research. In the meantime, we perhaps can only marvel that millions of years of natural selection on animals and a few centuries of experimentation with machines have resulted in an empirical and evolutionary solution to the problem; Group 2 motors have converged on a common upper limit of force output per unit mass, and this occurs in a manner that is surprisingly independent of mechanisms or material composition. Understanding why this is so may hold the key to further advances in motor performance or, alternatively, to the conclusion that an upper limit has been reached already.

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- Tesi, C., Colomo, F., Nencini, S., Piroddi, N. & Poggesi, C. T. (2000) *Biophys. J.* 78, 3081–3092.
- Brandt, P. W., Colomo, F., Piroddi, N., Poggesi, C. & Tesi, C. (1998) *Biophys. J.* 74, 1994–2004.
- 24. Josephson, R. K., Malamud, J. G. & Stokes, D.R. (2000) J. Exp. Biol. 203, 2667–2689.
- 25. Marden, J. H. (1987) J. Exp. Biol. 130, 235-258.
- 26. Marden, J. H. (1990) J. Exp. Biol. 149, 511-514.
- 27. Lehmann, F.-O. & Dickinson, M. H. (1997) J. Exp. Biol. 200, 1133-1143.
- 28. Full, R. J., Blickhan, R. & Ting, L. H. (1991) J. Exp. Biol. 158, 369-390.
- 29. Blob, R. W. & Biewener, A. A. (2001) J. Exp. Biol. 204, 1099-1122.
- Biewener, A. A., Blickhan, R., Perry, A. K., Heglund, N. C. & Taylor, C. R. (1988) J. Exp. Biol. 137, 191–205.
- Ritter, D. A., Nassar, P. N., Fife, M. & Carrier, D. R. (2001) J. Exp. Biol. 204, 3053–3064.
- 32. Luhtanen, P. & Komi, P. V. (1980) Eur. J. Appl. Physiol. 44, 279-289.
- 33. Webb, P.W. (1979) J. Exp. Biol. 79, 245-263.
- 34. Webb, P.W. (1978) J. Exp. Biol. 74, 211-226.
- McMahon, T. A. & Bonner, J. T. (1983) On Size and Life (Scientific American, New York).
- Kobayashi, M., Wakiwaka, H., Watanabe, M., Mizuno, H., Karita, M., Maeda, M., Matsuura, Y., Fukunaga, S. & Yamada, H. (1996) *Artif. Organs* 20, 1320–1324.
- 37. Chai, P. & Millard, D. (1997) J. Exp. Biol. 200, 2757-2763.
- 38. Alexander, R. M. & Jayes, A. S. (1983) J. Zool. 201, 135-152.
- Brechet, Y. & Lebyodkin, M. (1997) in *Scale Invariance and Beyond*, eds. Dubrulle, B., Graner, F. & Sornette, D. (EDP Sciences, Berlin), pp. 107–118.
  Epstein, A. H. & Senturia, S. D. (1997) *Science* 276, 1211.