

12. Invertebrate locomotor systems

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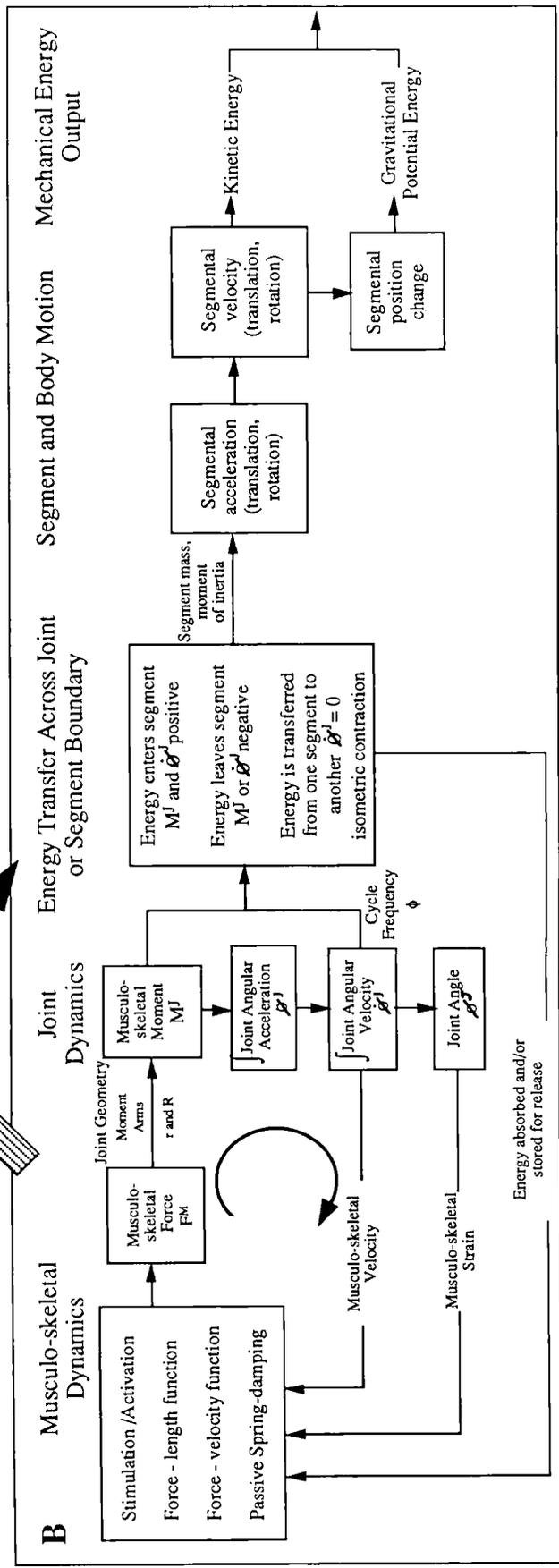
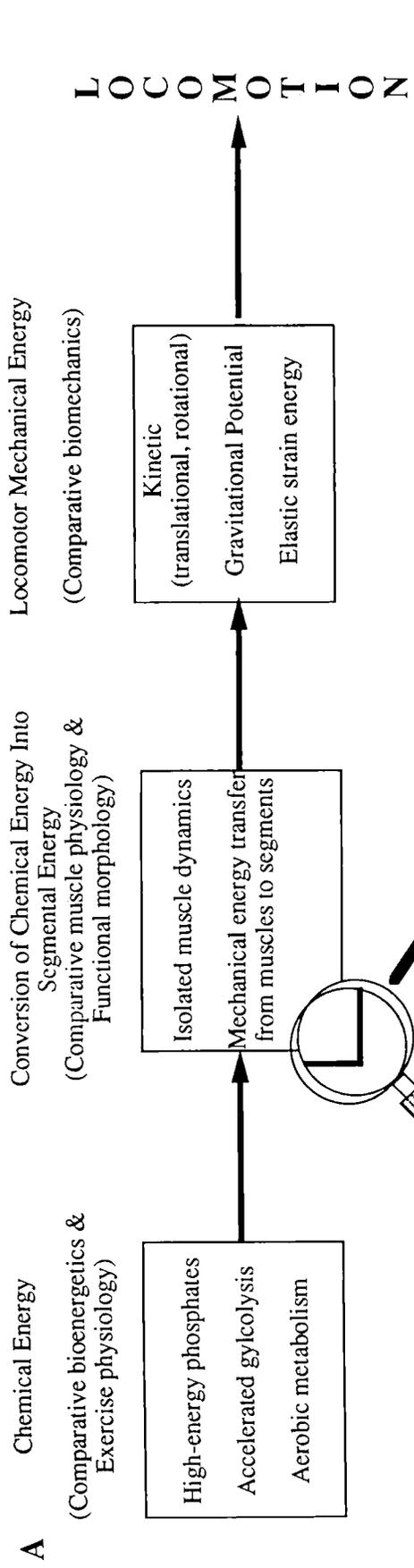
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Appendix: List of Symbols

ORGANISMAL BIOLOGY is entering an exciting new era of integration following the maturation of specialized fields. Comparative physiology, broadly defined to include functional morphology and comparative biomechanics, sits in an opportune position with respect to its level of biological organization. Being between molecular biology and behavioral ecology offers the possibility of linking molecular function to relevant whole-animal performance and behavior in the field. The technologies of rapid data acquisition, analysis, imaging, and computer modeling will allow unprecedented advancements in the future because the overwhelming complexity involved in system integration can be addressed for the first time.

Why study locomotion? First, locomotion is one of the best behaviors to study from a systems viewpoint because the integration of systems is so evident. Musculoskeletal systems—hydrostatic and jointed framework—which produce movement, nervous and endocrine systems that control movement, and circulatory and respiratory systems that sustain locomotion, are often interdependent. I discuss the conversion of chemical energy in muscle cells to the mechanical energy that the whole animal generates for locomotion (Fig. 12.1).



This requires a synthesis of information from the fields of comparative bioenergetics, comparative muscle physiology, functional morphology, comparative exercise physiology, and comparative biomechanics. Second, locomotion is central to the behavior and function of nearly all animals during at least some phase of life, so general comparisons are possible among diverse species.

Why study invertebrate locomotion in particular? First, the typical, or representative, animal on Earth, if there is one, must be an invertebrate. Three-fourths of the world's animals are insects. Second, nowhere is there greater diversity within a group. The number and variety of arthropods alone exceeds that of vertebrates by 100-fold (217). Basic design principles become clear when we examine diverse systems with extreme functional demands. "Natural" experiments can be conducted by the selection of appropriate species using a comparative approach in a phylogenetic context. The variation in locomotor parameters as a result of evolution is far greater than can be attained by any direct experimental manipulation. Variations due to size, mode of locomotion, species, and temperature allow a wide variety of hypotheses to be tested that might otherwise be untestable. Third, invertebrates exemplify the Krogh principle: "For many problems there is an animal on which it can be most conveniently studied" (332). The relative simplicity and ease of manipulation of invertebrate systems are assets. For example, some insect muscles are innervated by a single nerve that produces an electromyographic (EMG) signal with a single spike. An isolated muscle preparation can function aerobically for long periods of time if the trachea are intact since the circulatory system is not required for oxygen delivery. In a more practical vein, invertebrates are often easily attainable and inexpensive to purchase and house. Because of their size, they occupy little space. One can have a muscle physiology, whole-animal exercise physiology, and biomechanics laboratory in a single room. Fourth, invertebrates are excellent systems for the direct study of the evolution of locomotor traits. Many have short generation times. Genetic manipulations of muscle structure and function

have already been accomplished and offer a tool for testing function (493). Fifth, invertebrate locomotion and energetics are becoming increasingly important in ecology, where we seek an understanding of the spatial and temporal patterns of the distribution of animals. Invertebrates are important in disease and can act as biological control agents, so an understanding of invertebrate locomotion is of obvious economic importance. Finally, data on invertebrate locomotion can serve as biological inspiration to those studying artificial intelligence and control, mechanics, and robotics from the nano- to mesoscopic scale in particular (193).

No review of invertebrate locomotion can be truly all-encompassing. Yet, showing only single examples, case studies, or model animals fails to represent the diversity of systems available for study. The case study approach may inhibit integration in the future. Instead of listing each group and describing its mode of locomotion, I put the information in a framework based on energy to facilitate comparison and integration of muscle function, bioenergetics, exercise physiology, and biomechanics (Fig. 12.1). As a result, I have restricted my discussion to those groups for which more complete biomechanical and physiological analyses have been made.

To provide a more quantitative comparison, I have extracted numerous values from the literature. The data selection process was extremely difficult, and nearly each point can be disputed by some criteria. I err on the inclusive side. I accepted data unless there was an undisputed, independent reason for not including them. In this way, future investigators can more easily find particular studies and provide their own evidence to reject or corroborate the general relationships presented here derived from the data sets.

Discussion at nearly any level will be introductory to the experts and too advanced for those from other fields. I apologize to the experts and suggest some extraordinary books and reviews as a general introduction to invertebrate locomotion for fresh minds (10, 11, 14, 16, 17, 19, 66, 166, 221, 232, 258, 286, 315, 357, 406, 472, 485, 489).

After a survey of the different mechanisms used

FIG. 12.1. Schematic diagram showing integration of comparative bioenergetics, exercise physiology, functional morphology, muscle physiology, and comparative biomechanics. *A*: Energy available from several sources is transduced to segments (appendages or body sections) through muscles, depending on geometry. The chapter is organized in sections from right to left. *B*: Magnification of musculoskeletal role in transducing energy. Musculoskeletal parameters determine musculoskeletal forces. Musculoskeletal forces and joint geometry determine moment. Moment gives rise to acceleration, velocity, and angle change. Velocity and angle change (change in muscle length) feedback to affect musculoskeletal force production. Moment and joint angular velocity determine amount of energy transferred. Direction of movement and moment determine whether energy enters, leaves, or is transferred from a segment. Segmental energy and morphology of all segments determine power output of whole body and represent locomotor mechanical energy in *A*.

in invertebrate locomotion, I examine the common mechanical variables from diverse species using different modes of locomotion as a function of body mass. Next, I examine isolated muscle dynamics, from the level of sarcomeres to energy transfer into the segments, (for example, femur of leg, slice of wing, section of paddle) used during locomotion. I follow with an examination of the metabolic cost of locomotion and its relationship to endurance. In essence, I follow the outline diagrammed in Figure 12.1A in reverse. I conclude by offering a general integrative hypothesis of invertebrate locomotion based on data in the literature.

MECHANISMS OF LOCOMOTION

The diversity of locomotor mechanisms used by invertebrates is spectacular. A complete description of the multitudes of mechanisms would require volumes. To provide a glimpse of the rich diversity, I mention several broad categories of invertebrate movement: swimming, crawling, running, jumping, and flying. In doing so, I summarize major reviews and articles in comparative biomechanics that go beyond a verbal description. It is the study of comparative biomechanics that integrates the behavior and movements we see with the energy involved in making those movements. It is the mechanical energy associated with bodies and appendages that sets the range of operation of the musculo-skeletal system. Despite the seemingly overwhelming diversity of locomotor modes, biomechanics supplies the appropriate quantifiable variables that are general enough to allow comparison. After a discussion of the modes of locomotion, I use variables such as speed, frequency, and mechanical power output to make comparisons among the modes of locomotion with respect to differences in species, body size, and temperature.

Swimming

Invertebrates swim by undulating their bodies; rowing with cilia and paddles; jetting with body cavities, shells, bells, and rectums; flipping their tails; skimming with secretions; and hopping and flying under water. The propulsive thrust for swimming results from the momentum exchange between the active motions of the propulsive surfaces of an animal and its surrounding medium. A general relationship describing force and water flow for an element of fluid near a moving animal is given by the Navier-Stokes equations (131). The change in momentum of a small element of fluid is due to differences in pressure stress, viscous stress, and the net force acting on the animal. The complete Navier-Stokes equations exclude the development of

analytical solutions. Computational schemes have been devised for specific situations, but they can be restrictive and mathematically cumbersome (131).

Traditionally, comparative biomechanists and physiologists have made two simplifying assumptions that allow analytical solutions. In large, fast swimmers, viscous stresses are taken to be negligible. At these high Reynolds numbers ($Re = \text{inertial/viscous forces} = u L^S/\nu$, where u is swimming velocity, L^S is a characteristic length, and ν is kinematic viscosity), swimming is dominated by inertial stresses, where drag (D) and lift (L) are determined as follows:

$$D = 0.5 C_D \rho A u^2 \quad (12-1)$$

$$L = 0.5 C_L \rho A u^2 \quad (12-2)$$

C_D is the dimensionless coefficient of drag parallel to the swimming motion, ρ is density of water, A is area, u is velocity, and C_L is the dimensionless coefficient of lift perpendicular to motion. In small, slow swimmers, inertial stresses are taken to be negligible. At these very low Re , swimming is dominated by viscous stresses. At intermediate Re , one must rely on experimentally defined dimensionless coefficients of drag and lift, where the exponent of u is between 1 and 2. I briefly discuss swimming at low Re ($\ll 1$) and then follow with summaries of swimming mechanisms at high ($>1,000$) and intermediate ($1 < Re < 1,000$) Re .

Low Reynolds Numbers ($Re \ll 1$). When viscous forces dominate movements, swimming can be described by simpler equations, referred to as Stokes equations (131). The relevant forces for locomotion result from fluid shearing. Because inertia is lacking, lift and jet reaction mechanisms simply do not work as well because the predominance of viscous shearing overwhelms such inertial processes. If an animal stops swimming in an environment dominated by viscous forces, it will stop almost instantaneously.

At low Re , thrust is generated by viscous shearing resulting from asymmetric motion. Reciprocating structures that operate symmetrically generate no net force. Since viscous flow processes are described by linear equations, slow motions over long periods of time have the same effect as fast motions over short periods of time. Forward progress cannot arise from swimming motions with fast power strokes and slow recovery strokes if the propulsor geometry does not change between strokes. Motion must have asymmetry since changing the speed or power of the structure alone will generate no net thrust. Drag at low Re is dependent upon surface area and can be estimated:

$$D = k_{vis} \mu L^S u \quad (12-3)$$

where k_{vis} is a constant that depends on shape and orientation, μ is dynamic viscosity, L^s is body or segment length, and u is velocity (10).

Species

Protozoans, single cells, small worms, and the larvae of many marine invertebrates swim at low Re. Cilia or flagella typically provide the propulsion, but undulatory locomotion is common in small worms (275). Since this chapter emphasizes muscle function as the originator of propulsion, a summary of low Re research is beyond its scope (but see refs. 131, 274, 440, 485, 527). Nevertheless, it is important to mention a few principles so that the problems of describing swimming at intermediate Re can be better appreciated.

Flagellar thrust has been successfully predicted for swimming at low Re in sea urchin spermatozoa (233). Given a long, thin, cylindrical shape, equation 12-3 can be used to calculate the sum of the forces produced by many small, straight cylinders. These cylinders are oriented at an angle such that they form a part of retrograde waves (that is, rearward traveling) that generate a resistive force perpendicular to the direction of the cylinder's motion. Since transverse forces tend to cancel, the organism is pushed forward. This resistive theory of swimming (233) applies to very long and slender bodies; therefore, the term "slender body theory" has been coined to encompass such flow problems. The resistive force theory accurately predicts the hydrodynamics observed, except when the swimming motions become large in amplitude, when the organism swims near a boundary, or when propulsors are closely packed, such as with cilia (131). The resistive theory neglects up- or downstream effects of adjacent segments or surfaces.

Larger organisms using thousands of cilia can swim tenfold faster than others at low Re (440). Cilia beat in an asymmetrical manner such that they are straight on the power stroke and bend on the return stroke. Because of the cilia's close proximity to each other, models of independently beating cilia do not predict whole-organismal performance. Three different models are used to describe the hydrodynamics of ciliary propulsion: the envelope, sublayer, and traction models (131). These models show that effective ciliary locomotion requires the number of cilia to be much greater than the ratio of body length to cilium length (440). Since the number of cilia decreases with an increase in body length, larger ciliates have a lower hydrodynamic efficiency.

CTENOPHORES. The largest organisms to use ciliary locomotion are comb jellies which actually move at intermediate Re (364). They use giant cilia (2 mm in length) that are grouped in rows or plates and run the

length of the body. The whole ctenophore operates at Re of 100–6,000, whereas the cilia move at Re of 10–300. The arrangement of the plates smooths out intermittent flow from individual units and imparts a greater momentum to the water than would be attained by single plates because the plates can cooperatively capture partly accelerated backflow from around other plates (31, 32).

High Reynolds-Numbers (Re > 1,000). If an animal stops swimming in a high Re environment, it visibly glides to a halt. At very high Re, viscous terms disappear and flow is best described by the Euler equations. These equations describe fluid forces that arise entirely from pressure and accelerational terms rather than from any viscous shearing (131, 341). Euler equations state that accelerations of the fluid yield pressure gradients in that fluid (131). Because no true propellers or paddlewheels have been found among animals, invertebrates undulate or oscillate parts of their body or appendages to generate thrust. Thrust results from the balance of at least five forces: pressure drag, lift, added-mass forces, squeeze or jet forces, and inertial forces.

Drag is the resistive force that opposes motion (that is, speed). Because of its dependence on velocity, drag resists accelerations and augments decelerations. Drag-based propulsion results when an appendage or section of a body moves backward and the water resists that movement. Lift can be created if an appendage operates as a hydrofoil. Added mass force is the reaction to acceleration itself (129, 142). Appendages or bodies are accelerated along with a mass of fluid around them. As a result, the mass of the appendage or body appears as if it were a larger mass moving. The added-mass force resists both accelerations and decelerations of bodies and appendages. Thrust from added-mass forces results from the water's reaction to rearward accelerating appendages or bodies and the water that moves with them. Squeeze or jet forces arise from the pressure created as fluid is squeezed out from the space between parts of bodies, between appendages, or between the body and appendages. Finally, inertial forces can also accelerate, decelerate, or rotate the body.

For larger paddlers and rowers operating at higher Re, a quasi-steady analysis of resistive forces (drag and sometimes lift) tends to work well for predictions of whole-body forces, even though unsteady forces (such as added-mass forces) can be present (131). The forces produced by undulators or very rapidly oscillating appendages, however, depend largely on added-mass forces. Unsteady forces become very important during intermittent and escape swimming. Squeeze or jet forces are particularly important in jet propulsion (for example, jet reaction in medusae, salps, and shrimp).

Invertebrates should be used in future studies that consider these forces and the relatively unexplored interactions between body sections, between appendage sections, and between the body and appendages (340, 526).

Undulation

Using Euler's equations, Lighthill (341) showed that thrust can come from acceleration of fluid relative to the body. Since a rod moving broadside has a greater added mass than one moving lengthwise, a section of an undulating body that accelerates laterally at some angle produces a reaction in the fluid to that acceleration. The reactive force has a component in the direction of thrust. The force on a section of the body depends on the change in lateral velocity of the body and its mass (including added mass). All of the sectional reaction forces, when integrated over the surface of the body and averaged in time, are manifest as a specific rate of momentum shedding from the trailing edge of the body. This shedding of momentum is the core of Lighthill's (341) slender body theory, whereby average thrust depends on the rate at which momentum is shed from the rear end of the animal or the trailing edge of the retrograde undulating wave (131). The hydrodynamic efficiency (η) of using undulating waves is equal to the ratio of useful work to total mechanical work:

$$\eta = (1 - u)/u^W \quad (12-4)$$

where u is forward speed and u^W is the speed of the rearward propagating wave. In general, efficiency is greatest when a large amount of fluid is accelerated more slowly per unit time than if a smaller mass is accelerated to a higher velocity. Euler's equations suggest that body shape and the extent of lateral undulation can affect thrust. Long bodies that flatten to a greater degree posteriorly can increase thrust. Large lateral accelerations increase thrust, but when the amplitude of undulations gets very large, slender body theory can be violated because these accelerations may affect flow in regions upstream from the trailing edge. Future study of undulation will depend on computational fluid dynamics so that large amplitude movements, whole-body accelerations, and complex geometries can be examined (131).

SPECIES. Most undulatory swimming invertebrates use retrograde waves. Waves are generated by the body or by undulatory movements along the body's edge. Some species are assisted by appendages (for example, parapodia).

1. Annelids. Polychaete worms, such as *Nereis*, swim by an extension of rapid crawling. In contrast to crawling, they undulate side to side, but the body waves travel forward (116). The waves are direct (that is,

they travel forward) and the amplitude and length increase with speed. *Nereis* has large flap-like parapodia projecting from the sides of the body. Parapodia carry out backwardly directed power strokes at the crest of each wave and assist in movement by rowing. Without parapodia, the direct wave of *Nereis* would most likely yield backward motion. The hydrodynamic forces acting on the parapodia appear to be larger than those acting on the body. In most undulatory swimmers, retrograde waves generate a large normal force (perpendicular to the segment) as the segment pushes back against the water. Parapodia increase the axial force component (along the segment) as opposed to the normal component. Because the forces on the parapodia are at right angles to the body, forward waves can push the worm ahead. The parapodia act like "roughness elements" or flimmer filaments in flagellates (10).

Leeches are cylindrical when crawling but dorsoventrally flattened when swimming. Muscles that run dorsoventrally flatten the leech, whereas dorsoventral longitudinal muscles operate 180° out of phase to generate the body waves (472). Waves travel backward to propel the animal forward.

2. Molluscs. Gastropod molluscs with developed feet can produce one or two undulatory waves within a body length (*Aplysia*, 472). Cuttlefish (*Sepia*) swim slowly by undulating fins that produce waves (138, 325).

Hydrofoils

For many animals, thrust may arise from lift rather than drag or added-mass forces. In an aquatic environment, appendages act as hydrofoils flapping in a plane perpendicular to the motion of the animal. Lift forces arise from a pressure asymmetry between the top and bottom of the foil, with low pressure at the top. The net force from the pressure asymmetry contributes to thrust if the appendage has a mean positive angle of attack.

SPECIES

1. Crustaceans. Hydrofoils appear to be used in the sideways swimming of blue crabs (409). The rearmost legs on both sides of the body are paddle-like and the crabs can swim at 1 m/s, paddling at 4 Hz. They operate at Re ranging 63,000–190,000 for the body and 18,000 for the paddle. The swim paddle is a fairly typical animal wing. Lift and thrust may be produced on the fore- and backstroke. The rear legs move in the same direction (forward and backward) at the same time, but one leg is on the upstroke while the other is on the downstroke.

Blue crabs have also been reported to hover with little lateral movement (409). In hovering, the rear

legs beat differently from the way they do in forward swimming and have two patterns. The paddle can sweep back and forth at 2 Hz in short horizontal arcs or it can use more sweeping vertical arcs. Hydrodynamic efficiency may be increased by operating close to the ground due to a ground effect (that is, forces induced by overlapping boundary layers).

Scyllarid lobsters that can swim continuously have very broad, flattened carapaces, short antennae, and recessed eyes. Significant lift can be generated by the body acting as a hydrofoil during repeated backward tail flips (294).

Jet Propulsion

Jet propulsion is used by several invertebrate taxa. In each case, water is expelled in one direction to propel the animal in the opposite direction. There are few continuous jetters, only those that operate periodically (497). A cycle of jetting can be broken down into a power and a recovery stroke. During the power stroke, thrust (T) can be produced by drag-based propulsion, added-mass forces, and squeeze or jet forces. Effective jets depend upon the velocity and mass of water ejected, the mass of the animal, and the magnitude of drag forces. The velocity (u_{jet}) and mass of water ejected depend upon the capacity of the chamber and the area of jet aperture (A^A). The greater the aperture and pressure produced, the greater the thrust:

$$T = 2 C_{\text{dis}} A^A \sigma_{\text{jet}} \quad (12-5)$$

where C_{dis} is the coefficient of discharge and σ_{jet} is pressure (303, 473). Unfortunately, this equation assumes a constant aperture area. Alternatively, thrust can be calculated from flow rate, where

$$u_{\text{jet}} = (2 \sigma_{\text{jet}} / \rho)^{0.5} \quad (12-6)$$

$$T = \rho u_{\text{jet}} Q \quad (12-7)$$

and u_{jet} is the jet velocity and Q is flow rate through the funnel (396). Pressure is then

$$\sigma_{\text{jet}} = 0.5 \rho (Q/A^A)^2 \quad (12-8)$$

The duration of jet pulse is dependent on the jet aperture if all else is constant. During normal swimming, apertures are often constricted to produce a longer pulse. During the recovery stroke, jetters must restore fluid and extend contracted muscles. There is evidence in some groups that elastic properties may aid expansion (see under Muscle–Organismal level below).

SPECIES

1. *Coelenterates*. Medusae and siphonophore bells use subumbrellar muscles to contract and expel water downward (473). During recovery, water is drawn into a cavity by the reaction of elastic mesoglea. Relatively

small pressures are generated [for example, 20–30 Pa (139)], which results in slow swimming velocities [*Carybdea*, 0.02 m/s (473)]. Larger species (for example, *Stomolophus meleagris*) can attain masses of 1 kg and swim at 0.15 m/s (338).

A hydrodynamic model of medusan jet propulsion shows that the largest instantaneous forces produced during swimming are derived from the acceleration reaction but that in steady swimming their average contribution is zero (128). In escape swimming, the acceleration reaction is the dominant force and use of contraction times near 0.1 s may optimize accelerations given energetic constraints. The model of Daniel (128) predicts that steady swimming velocity and energy cost are optimized using a duration of relaxation to contraction of approximately two. DeMont and Gosline (141) have shown that jellyfish function as harmonically forced, damped oscillators that operate at their natural frequency.

2. *Molluscs*. Cephalopod molluscs, like squid, are spectacular jetters (473). They have separate inhalant and exhalant apertures to move water in and out. Circular muscles contract to produce the power stroke as the mantle thickens. Radial muscles contract to thin the mantle and extend the circular fibers to draw in water. Fin thrust is important only at low speeds.

The hydrodynamics of jet propulsion in squid has been analyzed, assuming steady forces and a rigid body (303, 396). Added-mass forces may not be a major factor in squid swimming at high speeds because they cancel. Therefore, the standard drag equation (equation 12–1) and equations 12–5 to 12–8 have been used successfully. In the squid, *Loligo*, circular muscle can shorten by 30% and produce 30 kPa pressure developed at a stress of $1.5 \times 10^5 \text{ N} \cdot \text{m}^2$ (473). Oceanic squid can generate pressures of 50 kPa for jetting (473). Powerful jetters, such as *Loligo*, have strong muscles and a large mantle cavity, whereas weak jetters, such as the octopus, have small mantle cavities. In squid, a large percentage (30%–90%) of total force for jet propulsion is required to be hydrodynamic lift, to balance a negative buoyancy (396).

In the recovery stroke, 1.5 kPa negative pressures can be seen in the mantle of *Sepia*, facilitating water intake during fast swimming. As speed increases, the force production necessary for refilling increases from 3% to 20% of the total (396). The cost of accelerating water into the mantle cavity at high speeds has been previously underestimated. For large squid swimming fast, flow-induced negative pressures could assist in refilling (487). Likewise, mantle springs can also aid in powering refilling (226).

Molluscan jetters have exhaust ratios (mass of propellant:total mass) of 1:10 and Froude efficiencies (use-

ful power:total power) of half of those of fish (105). Squid and cuttlefish (exhaust ratios = 0.5–0.6) are capable of generating more thrust than *Nautilus* and octopus [exhaust ratios = 0.14–0.17 (105)]. Squid can burst and coast or climb and glide and potentially save 35%–60% of the energy used in horizontal swimming (396).

Scallops, such as *Pecten* and *Chlamys*, swim by jet propulsion using repeated adduction of their shells (381). The pressures generated are as great as 3–4 kPa in *Chlamys* (362). Scallops can expel as much as 50% of their body volume during each jet cycle. In general, expulsion of large volumes of water at low pressure is most economical. Elastic properties of abduction aid expansion of the shells by storing elastic strain energy in the hinge (8). DeMont (137) has demonstrated that swimming scallops function as a resonant system in which the muscles do little work to move the shells because they must simply overcome damping. Vogel (486) has argued that flow-induced phenomena can assist in shell reopening.

3. *Insects*. Dragonfly larvae, such as *Aeshna*, swim by ejecting water from a specialized rectal chamber (473). Pressure can reach 6 kPa when swimming at 2 Hz. This compares well with cephalopods, given the size differences. Examinations of the musculoskeletal arrangement are consistent with the possibility that elastic properties aid expansion of the anal region (377).

4. *Crustaceans*. Shrimp and lobsters can swim with a rapid flexion of the abdominal muscle, producing a backward tail flip. Swimming is cyclic, but an escape response can include only one or two contractions (494). Thrust from a rapid flexion of the tail in the escape locomotion of the dock shrimp is dominated by accelerational (that is, added-mass) forces early in the jet or single stroke (132). The force required to squeeze water out from between the body and abdomen dominates at the end of flexion. Propulsive drag force is small compared to reactive and squeeze forces. If squeeze forces were not considered, thrust would be underestimated by one-half to one-third.

5. *Tunicates*. Salps jet by rhythmically contracting the muscle bands in their body wall (73, 351). They possess separate inhalant and exhalant apertures. The contractions close the inhalant aperture before body wall muscles contract to expel water posteriorly (350). Elastic properties may assist expansion since the integument antagonizes the muscle bands of the body wall.

Rowing

In rowing, appendages function as oars or paddles that drive masses of water backward. The power stroke must generate greater force than the recovery stroke.

In most cases, the greater force is a result of a shape change. Appendages tend to be broadside during the power stroke and edge-on during recovery (10). The oars must give backward momentum to the water at the same rate as the body gives forward momentum to the wake to maintain constant speed. Less power is necessary if the animal accelerates large masses to a low speed than smaller masses to a high speed. Thus, large oars tend to be more efficient. Rowing appendages are usually paired and move in synchrony such that lateral forces cancel, but other gaits have been reported.

SPECIES

1. *Insects*. Dyticid beetles, such as *Acilius*, are among the best studied invertebrate rowers (387, 389). Water beetles swim at speeds ranging from 5 to 50 cm/s at Re of 900–9,000, where inertia is important. The water beetle's hindlegs are flattened with an enlarged rowing surface and edged with hair-like setae, which make them paddle-like. The paddle changes shape because the setae spread during the power stroke and collapse during recovery. These underwater paddles propel the beetle forward because the power stroke thrust is greater than the counterthrust of the recovery stroke. Although the recovery stroke is faster than the power stroke, the thrust-generating area is greater in the power stroke. The power stroke impulse is 40 times greater than the recovery stroke. Sixty-eight percent of the drag on the leg is due to the setae (389). The broadest area of the paddle lies distally at two-thirds to three-fourths of the leg length, where the maximal useful force is predicted for beating legs, oscillating wings, and propellers. The paddle has high drag with minimal material and is analogous to a hydromechanical rake. The Re for the hindlegs is still relatively small so that added-mass forces (that is, accelerational mechanisms) may not be important in the aquatic beetles, as they are in larger rowers (131). Squeeze forces could be used to increase thrust when the paired paddles close toward the body. The proximal portion of the leg that moves with the body is slender, has no setae, and provides no propulsion.

Even though the hindlegs have a high drag coefficient during the power stroke, the body of the water beetle is fairly streamlined [$C_D = 0.38–0.43$ (389)]. The drag on the body is 2.5 times that on a well-streamlined body of the same cross-sectional area (10). Front legs fold into grooves in the body and, therefore, have a relatively small frontal area. Drag incurred by the lateral edges of the body appears to be important for stability.

Some heteropterans use their long hindlegs and swim upside down. Each stroke drives the animal downward, but it then rises passively due to its positive buoyancy

(389). Ants swim with alternating movements of the front legs, as in walking (middle and rear legs are not used) (151), whereas grasshoppers use their rear legs in synchrony, as in jumping (187).

2. *Crustaceans*. Isopods swimming at Re of 3,000 use an unusual gait in which all three pairs of abdominal appendages begin the stroke simultaneously (6): the third has a short power stroke, the second an intermediate stroke and the first the longest stroke. After the strokes, there is a pause until the next stroke. This interesting pattern may result from a compromise in function since the pleopods are also used in respiration.

Intermediate Reynolds Numbers ($1 < Re < 1,000$). At intermediate Re , neither inertial nor viscous forces are negligible (131, 485). Drag, wakes, and unusual flows take time to develop. Many small adult and larval invertebrates fall into this challenging Re range. At these Re , one must rely on experimentally defined coefficients of drag (C_D) parallel to the swimming motion and lift (C_L) perpendicular to motion (see equations 12-1 and 12-2). Fortunately, computational techniques are being developed that may better deal with this Re range (183).

Undulatory Swimming

SPECIES

1. *Chaetognaths*. Undulatory swimming in chaetognaths demands a combination of low (viscous stress) and high (inertial stress) Re assumptions (307). These small marine worms (*Sagitta elegans*) swim at Re of about 100, by rapid dorsoventral undulations using a long slender body and fins. At the initiation of swimming (first 200 ms), inertial theory works well. Inertial stresses are large at the onset of swimming but decay rapidly. Viscous stresses dominate as the swimming motion approaches a steady state. Thrust is dominated by resistive components even when inertial stresses are 100-fold greater than viscous stresses.

2. *Nematodes*. Nematodes possess a cuticle with longitudinal but no circular muscles (472). Dorsal and ventral longitudinal muscle groups contract in opposite phase and a retrograde wave is generated. Wave amplitude increases as the waves pass posteriorly along the body. Locomotion of nematodes, such as *Panagrellus*, *Rhabditis*, and *Tubatrix*, at Re of 4-10, is highly dependent on the medium and the suspension of particles (234). Some species move by the production of three-dimensional helical waves when viscosity is increased.

Nematodes have helical fibers in their cuticle. The cuticle appears to be antagonistic to longitudinal muscles. Worm models suggest, however, that energy can-

not be stored and returned by these fibers (13). To recover elastic strain energy, strain energy must be stored as the animal is bent and decrease as it is straightened. The animal would have to be stable in the straight position and would tend to straighten by elastic recoil when bent. When some worm-like models are bent, their fibers slacken and strain energy is lost. *Ascaris* is usually bent into wavy curves and may be more stable in this configuration. Yet, some worm models do not account for noncircular cross-sections, which may be using other load-bearing elements to maintain their noncircular form (403). Models simplifying these fibers have produced locomotion comparable to that seen in the animal (394).

The large crawling nematode *Mermis nigrescens* does not use the classical undulatory pattern seen in swimming (218). Instead, this nematode laces its body around fixed objects and applies a propulsive force as the body glides by the contact site.

3. *Oligochaetes*. The freshwater oligochaete *Dero digitata* moves in a unique way (150). A single helical body wave travels from the worm's anterior end to its posterior end at 6-12 cycles/s. These 14 mm worms travel at speeds of 25 mm/s and Re of 50-300.

Rowing

SPECIES

1. *Insects*. Rowing in the water boatman by synchronous movements of the hind legs occurs at intermediate Re ($Re=700$) (65). At these Re , inertial forces are important since accelerations and decelerations of the body are considerable. Unsteady added-mass force acts in the direction of forward motion over most of the stroke. The impulse of a forwardly directed added-mass force during the power stroke is significant and equal to half the quasi-steady resistive-thrust force. Hydrodynamic efficiency (equation 12-4) is 0.52. Propulsive cycle efficiency is twice that of drag-based fin rowing, which indicates that the boatman's legs are effective paddles. In general, at high speeds, rowing appears to be inefficient compared to undulation, but it may be more efficient at lower speeds.

2. *Arachnids*. Rowing in mites at Re of about 60 is interesting because of their gait. Most aquatic insects adapted for swimming use a stable method of propulsion: a pair of legs sweep in tandem (35, 443). This gait obviates the tendency to yaw. Aquatic mites swim by using four legs in diagonal phase synchrony. Leg pairs and legs on the same side of the body operate almost completely out of phase, as in terrestrial locomotion. This seemingly unbalanced propulsion results in little wobble because the two pairs of paddles are close together near the center of the mass, minimizing moments. The distance between the posterior pair of

legs is wider than that between the anterior set, and more thrust is developed by the posterior legs, and a broad power stroke angle reduces turning forces.

3. *Crustaceans*. The swimming of copepods and crustacean larvae can be coupled to their feeding (329). Rowing is accomplished by bristled antennae, modified mouthparts, and swimming legs (pereopods). Cheer and Koehl (111) showed that bristled appendages at these Re (50–1,000) can be used as paddles or oars for swimming and food capture but not as rakes for sieving and scrubbing food particles out of the water [although some paddles might be leaky, such as in *Daphnia* swimming (330)]. Hydromechanical models of copepods show that the legs can remain nearly stationary during a swimming hop; perhaps this process should be called underwater walking instead of paddling (386). The acceleration and deceleration of the body during typical nonsteady velocity swimming increases drag values over average speed estimates by one order of magnitude (385). Models also predict that 30%–75% of thrust is produced by accelerating the water entrained with the legs (that is, related to added-mass forces).

Rowing propulsion can change during ontogeny in *Artemia* larvae. Newly hatched *Artemia* use one pair of limbs to swim and show considerable oscillations in body velocity at low Re (for example, $Re = 2$), where propulsion is drag-based (516, 517). As they grow, cyclic accelerations and decelerations of the body are reduced as Re increases (for example, $Re = 37$) and inertial effects and unsteady forces become more important.

4. *Molluscs*. The pteropod *Clione limacina* has flapping lateral parapodia that propel the animal like wings at intermediate Re (429). A novel lift-generating mechanism similar to the “clap and fling” of insects (see later under Hovering, unsteady effects) may be used on the up- and downstrokes.

Crawling

Invertebrates crawl by using peristaltic and pedal waves and by loops, anchors, “galloping,” and “leaping.” In soft-bodied animals, contraction of one set of muscles is most often antagonized by another set acting through a fluid-filled, or a hydrostatic, skeleton (489). Contraction of one muscle can influence all others, unlike the situation in a rigid, jointed framework skeleton. Changes in one dimension can result in changes in another. In contrast to a jointed framework skeleton, where muscles can be in a relaxed state most of the time, hydrostats must maintain tonus of the body wall musculature most of the time or the animal becomes flaccid. Because of these complexities, models of crawl-

ing with waves (149, 322) and using hydrostatic skeletons (488) are in the early stages of development.

The muscles of crawlers are organized into sheets and bands rather than blocks attached to apodemes (166). Most commonly, muscles are confined to a membrane and are circular and longitudinal in form. Oblique and transverse musculature may augment function. In some species, such as nematodes, only longitudinal muscles are present.

Two types of hydrostatic skeletons are recognized: stretched-membrane and muscular (324, 326). In stretched-membrane hydrostats, the ratio of power output to mass is low, so fewer fast movements are observed (138). Muscular hydrostats have a skeleton in which the fluid is replaced by a three-dimensional array of closely packed muscles. The power output to mass ratio is large, so fast movements are possible. Animals with muscular hydrostatic skeletons are capable of finer control and localized bending.

Peristalsis. Studies in invertebrate locomotion have aided our understanding of peristaltic transport processes in general (165). Peristalsis has been defined as any muscular contraction moving along a radially flexible tube in such a way that each component wave of circular, longitudinal, or oblique muscular contraction is preceded or followed by a period of relative relaxation of all similarly oriented muscles within a given tubular segment (247). Many soft-bodied animals that use peristalsis are nonsegmented, but annelids using this mode of locomotion are completely segmented. At least two types of peristaltic locomotion have been recognized, based on segmentation and the direction of wave motion: (1) retrograde, nonoverlapping peristalsis of mostly fully septate animals (for example, earthworms), with body waves passing from front to back; and (2) direct overlapping peristalsis of animals with variable volume segments (that is, nonseptate), with body waves passing from back to front.

In both types of crawling, anchors function when circular muscles are extended and segments are dilated. Retrograde wave propulsion can occur in segmented and nonsegmented animals, but direct wave travel requires that fluid be displaced from the region undergoing movement. If reciprocal action of circular and longitudinal muscles with fixed volume segments occurs, the animal must be employing retrograde waves.

Retrograde Waves

In annelids, such as the earthworm *Lumbricus*, each segment is a separate watertight compartment of nearly constant volume. Contraction of circular muscles causes the segments to become long and thin. Contraction

tion of longitudinal muscles causes the segments to become short and thick. When segments are short and thick, they are anchored by friction. Waves of lengthening and shortening travel backward along the worm. The worm moves forward by lengthening an anterior segment to push itself forward. The region behind remains thickened, serves as a point of attachment, and exerts a backward force. A posterior segment shortens to pull the worm forward, and it then becomes anchored (10). Hydrostatic pressure in the coelom is the highest during elongation, and these forces are necessary to push the worm forward. Maximum pressures on the order of 37 kPa have been recorded (475).

The speed of crawling (u) that results from the peristaltic wave motion is calculated as follows:

$$u = q u^w \Delta L^s / L^s \quad (12-9)$$

where q is the fraction of elongated or nonanchored segments, u^w is the speed of the retrograde waves, ΔL^s is the distance a segment shortens, and L^s is the segment length when elongated (10). Crawling speed can be increased by increasing wave speed, making segments lengthen and shorten to a greater extent and increasing the fraction of segments that are extending. Since the relative shortening and the fraction of elongated segments are less than 1, the forward speed of the worm relative to the Earth must be less than the retrograde wave speed. Therefore, waves must travel backward relative to the Earth.

Direct Waves

In segmented polychaete worms with no septa (where fluid moves more freely) and unsegmented sea cucumbers, direct waves are produced by simultaneous contraction of circular and longitudinal muscles (10). Fluid is driven out of the segment during contraction. During relaxation, fluid is driven in from other segments. Segments are anchored when they are relaxed and at their greatest diameter. A contracting segment pulls the one behind it forward. The expanding segment behind the contracted segment pushes the contracted segment in front of it forward. These movements cause body waves to move forward. This technique is argued to be particularly useful in soft mud because a large area can be anchored. The highest peristaltic pressures are developed in nonseptate animals with direct waves because a segment is contracting both circular and longitudinal muscles at the same instant (165). Septate animals generate lower pressures but tend to be more stable in terms of resting pressure fluctuations.

The force exerted on the substratum equals the internal pressure times the area of application. Somewhat

surprisingly, measured forces exceed calculated forces by 85% in a direct wave genus, *Arenicola*, and by 145% in *Lumbricus*, a retrograde wave genus. The excess pushing force has been thought to be due to the intrinsic rigidity of the skeleton (165).

Two Anchors. Caterpillars and some other insect larvae move using two anchor points. First, they extend their body forward after anchoring their rear prolegs. The anterior true legs are then held in place while the body is bent so that the prolegs approach the true legs, forming a loop. The anterior end of the animal is extended forward as the cycle starts again. In blowfly larvae, the wave of contraction is about half of the body length. Speed is increased by a combination of an increase in frequency and step length (that is, cycle distance) (54). Possible advantages of this type of crawling include a greater cycle distance and less friction. It has been argued that caterpillar locomotion is really direct arching peristalsis (247). Peristaltic modes of locomotion represent more of a continuum of movement than distinct mechanisms.

Leeches crawl in a manner similar to caterpillars, except they use their anterior and posterior suckers as anchors and can form large loops (451). Leech looping can be characterized as retrograde, nonoverlapping peristalsis.

Pedal Waves. Molluscs, such as gastropods and chitons, crawl on one foot using muscular pedal waves. In some cases, the waves are in phase all across the foot; these are termed *monotaxic* (475). In other species, the left and right sides can be a half-cycle out of phase; these are referred to as *ditaxic*. Different wave types occur in species that generate retrograde waves (for example, the periwinkle *Littorina* and the limpet *Patella*) and direct waves (for example, the top shell *Gibbula*). Usually two or three waves are found on a foot, but the number can reach 19 in terrestrial snails (305).

Chitons rely on retrograde waves, whereas snails use direct waves (10). When the lengthened portions of the foot are anchored, the animal uses direct waves. A section in the front of the wave is arched, pushed forward, longitudinally compressed, reelongated, and placed flat on the substratum. When the shortened portions of the foot are anchored, the animal uses retrograde waves. A section is arched, elongated, moved forward, stopped, recompressed, and placed flat on the substratum (475).

Mollusc feet can secrete mucus, which acts as a glue (145). The foot produces forward and backward forces on the mucus. In a retrograde wave, the lengthened parts occupy a smaller area and the shearing stresses they produce are greater. If the stresses attain a certain

value, then the mucus under them yields and behaves like a liquid, which allows sliding. After a time, the mucus heals and returns to a viscoelastic solid. The mucus under the shortened parts of the foot behaves like a solid and the foot remains anchored. In direct waves the mucus yields under the shortened regions. The properties of pedal mucus can be used to bound the maximal speeds and sizes for gastropods (144).

Pressure fluctuations in the hydrostatic skeletons of gastropods are rhythmic and correspond to each wave of stepping. In whelks, 3 kPa peak pressures have been recorded during crawling, over a standing pressure of 1.5 kPa (82).

Other modes of muscular crawling include galloping, which has been described in several species of the snail *Helix* (475). The head of the animal is raised, protracted, and put down again, thus forming an arch about one-third the length of the foot. Two or three such waves are formed, but the animal still uses typical direct pedal waves in addition. Leaping also occurs, such as in *Strombacea*, where the operculum is used as a lever to push the animal forward. Other modes of crawling include the use of ciliary gliding by triclads (for example flatworms) at low speeds and peristalsis at faster speeds for escape (475).

Walking, Running, and Rolling

Legged invertebrates can walk, run, and roll. They can move forward, backward, and to the side. They travel on land, on the surface of water, under water, up and down hills, upside down, and on irregular surfaces. No mechanical robot has ever approached this level of performance. Thus far, arthropods have served as extraordinarily useful models for motor control, interlimb coordination, regulation of load distribution, and proprioceptive control (see chapter 11 by Arbas, Levine, and Strausfeld in this *Handbook*). Only a handful of studies have addressed what the nervous system controls, the dynamics of leg and body movement.

Gaits

Definition of Variables

Descriptions of leg movement patterns have been influenced by both history and technology. The study of legged arthropod locomotion dates back to the Italian physiologist Borelli (1685). At their earliest stages, studies of neural control did not demand a complete description of motion to test proposed hypotheses. Also, the lack of technology often made more complete kinematic descriptions difficult. In some cases, high-speed cameras (400–1,000 frames/s) are

required to capture rapid leg movements (60). Computer image analysis now makes three-dimensional, quantitative kinematics feasible. The inability to quantify locomotor dynamics [both motion (*kinematics*) and forces (*kinetics*)] has resulted in a variety of indices or variables with similar names but sometimes different definitions, making comparison of gaits among walkers and runners difficult.

I have adopted the convention used in the design of legged robots (370), where stride period (t_{cyc}) is the time to complete one cycle of leg movement; stride length (L_{stride}) is the distance the center of mass moves in a cycle; stride frequency (ϕ) is the rate at which segments are cycled and the inverse of the stride or cycle period; speed (u) is equal to the product of stride length and stride frequency; duty factor (β) is the fraction of time in a cycle that a leg (i) is in the support phase (that is, on the ground); phase (φ) is the fraction of a cycle period a leg (i) leads or lags another leg; and gait formula (g_f) for an n -legged animal is

$$g_f = (\beta_1, \beta_2 \dots \beta_n, \varphi_2, \varphi_3 \dots \varphi_n)$$

A more complete gait formula could include the initial position of the feet in the horizontal plane.

Type and Number of Gaits

The number of gaits used by arthropods is still unknown for at least four reasons. First, very few species have been examined in total, even though some have been characterized in great detail, like stick insects, cockroaches, and crayfish. Second, many studies of leg movement patterns in arthropods do not provide sufficient information to construct a complete gait formula. In many cases, only the ratio of protraction (p , return, recovery, or swing phase) to retraction (b , stance, support, or power phase) is known [p/b ratio, where duty factor = $(1 + p/b)^{-1}$]. This ratio has proved useful for neurobiologists but lacks the phase information necessary to determine the timing of leg movements relative to one another. In other studies, only the sequence of leg movements is reported and no information about the duty factor is available. Also, speed, stride frequency, and stride length are rarely all reported. Third, the pattern of leg movement in some species may change continuously with speed and frequency so that no discreet gaits are apparent. Fourth, the description of leg movement alone may be insufficient to define a gait (that is, both kinematics and kinetics may be required).

Manton (356) proposed three gaits, or “gears,” for arthropods based on the p/b ratio. A p/b of 1 or a duty factor of 0.5 is considered middle gear. High gear ($p/b > 1$, $\beta < 0.5$) is used during rapid locomotion, whereas low gear ($p/b < 1$, $\beta > 0.5$) is used to develop high

forces when moving in mud and climbing on rocks. The concept of gears is valuable, but data show that gears do not necessarily represent discrete gaits.

Wilson (518) proposed a model of insect walking in which a change in gait resulted from different overlapping sequences of metachronal waves. This simple and influential model explained many gaits with a change in only a single variable (power stroke or stance duration, *b*) but could not produce all gaits observed. In contrast to the metachronal model, the alternating tripod or tetrapod models assume two functional leg groups: L1 R2 L3 R4 and R1 L2 R3 L4, where L is the left and R is the right side (34, 79). Walking legs 1 and 3 on one side of the body move synchronously and alternate with legs 2 and 4 on the same side. Protraction and retraction both vary but with the ratio of the two remaining at about 1 and the phase between ipsilateral (that is, same side) and contralateral (that is, opposite side) legs near 0.5.

These and other models (122, 133, 136, 230, 512) have contributed significantly to our understanding of arthropod gaits and neural control. Yet, few general dynamic models have been produced. Therefore, I first summarize the general trends reported in association with gaits and follow with a description of several dynamic models which deserve more attention in the future.

Design Trends and Hypotheses. Because few quantitative models have been proposed and tested for terrestrial locomotion, I report only proposed trends in leg construction, function, and stepping pattern. Most of these observations have come from the extraordinary work of Manton (357) and are still considered hypotheses awaiting more rigorous testing.

Leg Construction

Due to the shorter distance between the base and the tip of the leg in the middle propulsive than at the beginning or the end of the stroke, a straight and stiff limb, as is found in some polychaetes, is not as effective as an extensible limb (as in *Peripatus*) or a jointed limb with more degrees of freedom (356). Extensions or jointed limbs allow the limb to follow a straight path and not slip. Some roboticists found this very problem when they used straight limbs in their first attempt at building a hexapod (for example, Genghis) (23). Since then, they have designed jointed legs, inspired from arthropods such as cockroaches, which produce a more linear step (63).

Legs operating in a vertical plane parallel to the body (that is, horizontal first joint axis for body–leg attachment, as found in many birds and mammals) are gravitationally loaded and muscles must bear part of

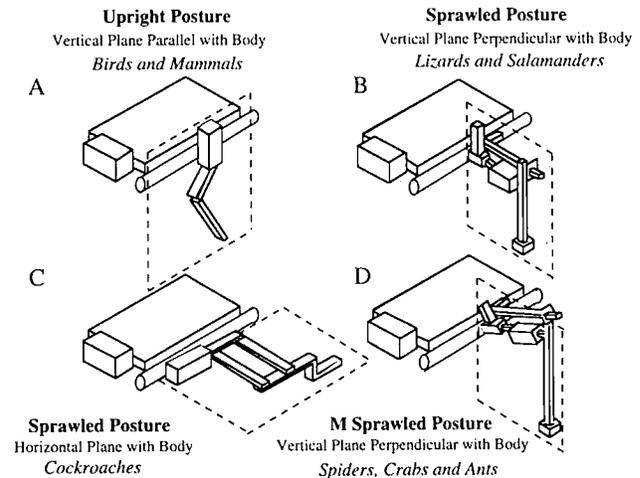


FIG. 12.2. Legs of animals in general, and of invertebrates in particular, can provide biological inspiration for the design of new robot legs. A: Legs operating in a more upright posture in a vertical plane parallel to the body (horizontal first joint axis for body–leg attachment), as seen in many birds and mammals, are gravitationally loaded and muscles must bear part of the body’s weight (24). Animals using a horizontal first axis, however, can take advantage of gravity in swinging their legs. B–D: Legs operating in a sprawled posture (vertical first joint axis for body–leg attachment, like some lizards, amphibians, and arthropods) can potentially decouple gravitational loading of muscles from moving forward. To move forward, vertical first axis legs must project out to the side, resulting in increased static stability. Robots inspired from the design of cockroaches (62, 63), whose legs operate in a horizontal plane, demonstrate a linear step, large step lengths, and proficiency at climbing (adapted from ref. 62).

the body’s weight (Fig. 12.2A) (24). Animals using a horizontal first axis can take advantage of gravity when swinging their legs. Legs in sprawled posture animals (that is, vertical first joint axis for body–leg attachment) can potentially decouple gravitational loading of muscles from moving forward (Fig. 12.2B–D). To move forward, vertical first axis legs must project out to the side.

Jointed legs that are stiff may be more advantageous than compliant ones if muscles transduce the force; however, spring-like legs may be important for locomotion at higher speeds (193).

Leg Length

Longer leg lengths can give a longer stride length than shorter legs and can result in an increase in speed. Also, longer legs increase the range of potential footholds. However, as leg length increases, the number of gaits possible decreases due to the likelihood of mechanical interference from overlapping fields of movement. Longer legs may require gaits to be executed more precisely and may demand more control.

Leg Number

The greater number of legs an animal has on the ground, the greater the degree of static stability possible. The animal's center of mass is more likely to be farther from the edge of the base of support if more legs are in the support phase. Also, greater force is available for pushing or burrowing if a greater number of legs are on the ground. However, as leg number increases, the number of gaits possible may decrease due to the potential of mechanical interference if the fields of movement overlap. Mechanical interference of walking legs can be reduced if leg number is lower, as in insects, arachnids, and some crustaceans, relative to millipedes and centipedes. However, with reduced leg number, fewer gaits may be possible if static stability is required (it is not always a necessity; see the discussion of stability later in this section). Regular precision in stepping may be unavoidable if the number of legs is reduced. Also, a reduction in leg number can lead to a decrease in the number of possible footholds.

Leg Location

For a sprawled posture with laterally projecting limbs, greater stride lengths can occur if the body is as close to the ground as possible. This tends to result in mechanical interference among legs. However, interference of legs can be reduced for long-legged animals if each leg is longer than the one in front or if a leg simply steps at a different lateral distance from the body. With the appropriate stepping pattern, legs will have a larger field of movement but will not collide.

Narrow or jointed legs can be placed on almost the same footprint as is occupied by the leg in front ("follow-the-leader" gait) but before the front leg is lifted. The weight of the body can be transferred to the leg immediately behind and not be borne by other legs. This can aid in static stability and prevent sagging of the body. Bodies have a tendency to sag if the propulsive legs are separated too widely.

Some arthropods possess leg pairs separated widely from one another (for instance, legs of stick insects are found anteriorly, posteriorly, and in the middle of the body). This placement tends to eliminate some of the problem of overlapping fields of leg movement. Joints of laterally projecting legs spaced far from the center of the mass, however, are more likely to experience larger turning forces (torques or moments) during locomotion than those placed nearer or in line with the center of the mass. If leg numbers are reduced and segments condensed so that long legs are attached to a fused segment like a thorax, then forces directed through the center of the mass can be aligned axially along the leg and point nearer the joint centers, thus

minimizing joint torques (197). Roboticists who have built a six-legged robot with identical legs placed only anteriorly, posteriorly, and in the middle of the body (for example, Attila) (23, 24, 63) have experienced some problems with torque motor failure. Recently, engineers have designed leg pairs that differ from one another and orient more toward the middle of the body (63).

Stepping Pattern

Even though all assertions in the gait analysis of legged invertebrates have exceptions, models have proved to be important in demonstrating the complex patterns that arise from a change in only a few variables (33, 79, 284, 289, 518).

Ipsilateral legs can move metachronally from rear to front if each leg moves slightly after the one behind or from front to rear if each leg moves slightly before the one behind. The phase of ipsilateral legs tends to remain the same or to decrease with speed. Pairs of contralateral legs tend to move in phase more often at slow speeds and one-half cycle out of phase at higher speeds. Ipsilateral leg coupling tends to be less variable than contralateral coupling.

The proportion of time a leg spends on the ground during each step (β) decreases as the speed of the animal increases and represents a shift from low to high gear. Duty factor tends to decrease and p/b to increase with stride frequency and speed. A decrease in duty factor may jeopardize static stability. Protraction times are relatively constant for faster speeds and on land, where support is important. Protraction time may vary for purposes of coordination when the legs are less involved in supporting weight (for example, in water).

SPECIES

1. *Onychophorans*. The onychophorans, presumably arising from a worm-like or annelidan ancestor, have an extraordinary locomotor mechanism (357). An increase in speed is accompanied by no lateral undulations, little change in stride period, a decrease in duty factor, and an elongation of the body (12%–24%), which increases stride length by allowing the legs to execute larger angles of swing since they are extensible. The bottom, middle, and top gears proposed by Manton (355) are observed in *Peripatus*. Leg pairs move in synchrony at slow speeds and in opposite phase at the highest speeds.

2. *Myriapoda*. The soft-bodied, millipede-like animal *Polyxenus* locomotes by mechanisms much like those of *Peripatus*. In general, millipedes have an elaborate bottom gear gait, which can increase power for pushing or burrowing (355). Duty factors are high and phase differences small. Leg pairs move in phase, and a wave

travels from tail to head. The large number of legs increases pushing force production.

Scolopendromorph centipedes have a top gear gait associated with high speed and show a considerable decrease in stride period, retraction time, and duty factor with an increase in speed (355). Speeds faster than those of onychophorans appear possible with a more rigid exoskeleton for muscle attachment. A leg posterior to another is not placed down before the leg in front is lifted, and sagging of the body can result. Metachronal waves of limb movement travel from head to tail. Two or three legs converge on a common footprint on one side of the body and form a focus or effective leg (20, 21). Each wave of limb and body movement passes through this focus because the waves are stationary with respect to the ground. Propulsive legs become farther apart, and body lateral undulations increase as speed increases. At the highest speeds of *Scolopendra*, just three of 44 legs support the body.

Scutigera morph centipedes are rapid runners which possess very long legs and multiarticulate plantigrade feet with relatively short body segment lengths (355). A phase difference of less than 0.5 results in legs that cross over one another in the recovery stroke. Legs differ by as much as twofold in length so as not to mechanically interfere with each other. Metachronal waves pass from the tail to the head, resulting in the divergence of propulsive legs and more evenly spaced points of leg contact. Lateral undulations of the body are nearly absent.

3. *Insects*. In general, most insects are said to have two gaits: a metachronal gait at very slow speeds and an alternating tripod at medium and fast speeds (0.03–0.80 m/s) (134, 135, 331, 534). Legs can be relatively long in some species, and very high speeds can be attained. Even though fewer legs are available compared to myriapods, crustaceans, and arachnids, the strides of adjacent legs may overlap. Interference is minimized because the leg contact areas are offset laterally.

In the development of a model of neural control, several apparent rules have been proposed to describe the gaits of insects at all speeds (289, 518): (1) ipsilateral legs move metachronally from rear to front, (2) protraction times are relatively constant, (3) contralateral legs move in antiphase with one another, and (4) the lag or delay between ipsilateral legs is relatively constant. A change in only the retraction time generates a series of stepping patterns that are speed-dependent. A decrease in the retraction time or stance period corresponds to an increase in speed and a shift from low to high gear, suggesting a fifth rule: (5) the proportion of time a leg spends off the ground during each step increases as the speed of the animal increases.

Duty factor decreases with stride frequency and speed, suggesting a sixth rule: (6) no front or middle leg steps before the one behind it has finished its forward movement. Patterns of leg movement like these in conjunction with outstanding neurobiological research have led to biologically inspired control systems used in many-legged robots (46, 122, 123).

These rules characterize the patterns of leg movement in insects remarkably well, but none is invariable. Cruse (121) proposed that waves pass from front to rear. Silverfish use a gallop of 20 cm/s, where leg pairs move in synchrony and the body is supported by a single pair of legs (358). Praying mantises actually use four legs during locomotion (78). American cockroaches can use only two or four during rapid running (208). Ants can use only four legs when trotting (535). Water striders use synchronous backward thrusts of middle or rear leg pairs (78). The elongated rear legs of katydids can step at half the frequency of the two shorter front pairs (228). Even though all of the assumptions and trends concerning insect locomotion have exceptions, the rules have proven to be an important demonstration of how complex patterns of leg movement can arise from a change in only a few variables (79, 284, 289, 518).

4. *Arachnids*. Arachnids were the first invertebrates to invade land, more than 400 million years ago (80, 519). Their gait has been described as two alternating waves of diagonally stepping legs, not strictly an alternating tetrapod. Duty factors decrease with speed and may differ among the legs. In scorpions and wolf spiders, the duty factor of leg 3 does not drop below 0.5 even when the other legs are approaching 0.33–0.4 (80, 258). It is hypothesized that leg 3 is disproportionately important in support or propulsion. Leg pairs tend to step in antiphase with one another, whereas ipsilateral legs show a variable phase (0.3–0.6) (80). Arachnid gaits are particularly interesting because many species lack leg extensor muscles. Leg extension is accomplished by pressure generated by the compression of the prosoma (68, 175, 404, 437).

5. *Crustaceans*. The most common gait for walking under water and on land in astacurans (for example, crayfish) and brachyurans (for example, crabs) follows the leg sequence 2, 5, 3, and 4. The pattern is a combination of an alternating and a metachronal gait, which is also common in spiders and scorpions (113). The stepping patterns in sideways traveling fiddler crabs can vary between leading and trailing sides (33). Soldier crabs, which walk forward instead of sideways, use the metachronal sequence 2, 3, 4, and 5 (441).

Surprisingly, phase may vary less with stepping frequency in crustaceans than in some other arthropods (113). Also, ipsilateral coupling appears to be less

variable than contralateral coupling. Power and return stroke duration can both be altered. Variation in power stroke duration, which is important in force equilibration and balance, is used to change speed (that is, duty factor decreases as in other arthropods). The timing between steps for coordination is regulated by the duration of the return stroke primarily when the leg is less involved in supporting weight, such as in water. Yet, *Ligia* can use exactly the same gait on land and in water (356).

Variation in Gaits

Variability and lack of stereotypy make it difficult to define general gaits in legged invertebrates. For example, Clarac (113) reported that steps in crustaceans are incomplete or repeated 25% of the time. Phase diagrams often show broad distributions (80). Data suggest that a wide variety of gait patterns appear to be used even within a gait sequence (298). A multitude of solutions to leg and body movement appear available. This conclusion, however, depends on at least two assumptions. First, since gait represents only kinematic data, all legs are assumed to contribute equally to movement. Yet, all legs are not identical nor do they function in a similar manner. Second, it is assumed that variation in stepping alone produces similar variation in whole-body movement. Blickhan and Full (69) found that whole-body oscillations of the center of mass in ghost crabs were remarkably consistent, despite considerable variation in the pattern of leg movements. These data suggest that gaits should be defined by determining dynamics (both kinematics and kinetics) of the legs and body.

Dynamic Models of Rolling, Walking, and Running. Very few quantitative investigations of the dynamics of invertebrate legged locomotion have ever been carried out. Yet, many have hypothesized about locomotor dynamics (357). Two themes are prevalent in the speculation. First, wheel-like movement (that is, reduced body accelerations and decelerations) is desirable and efficient. Second, static stability is a principal design constraint. These themes have received much attention and were an appropriate starting point because (1) the analyses were simpler, (2) wheeled vehicles were an intuitively appealing model, and (3) studies of neural control have focused more on large, slow animals that were the most desirable to study.

Rolling Like a Wheel

Manton (357) frequently referred to the importance of evenness in the body movements produced by various gaits. Gray (232) implied that the more legs an

animal has available, the more like a wheel it could function. Wheeled vehicles have smooth rides that are energetically efficient. Acceleration and deceleration of the body or center of mass are made negligible. Ground reaction forces are directed vertically toward the hub of each wheel.

Biologically, true wheels are difficult to construct. Moreover, wheels are not necessarily desirable because of their inability to function on all surfaces (335). To my knowledge, only one animal comes close to approximating a wheel, a stomatopod crustacean (85). This animal moves actively like a wheel for 40% of a roll or cycle as its body executes backward somersaults along the beach at 72 revolutions per minute (198). For most of a cycle, however, the stomatopod accelerates and decelerates with its entire body acting just like a single limb of legged animals.

The use of legs does not exclude the application of wheel-like dynamics (15). An important design criterion in the construction of multilegged robots is the minimization of energetic cost. This is accomplished by using legs which produce vertically directed ground reaction forces, reduce accelerations and decelerations of the center of mass, and provide a smooth ride. Yet, legged invertebrates do not appear to move like wheels (120, 229). They accelerate and decelerate their bodies both vertically and horizontally (69, 207, 208).

Walking and the Pendulum Model

The inverted pendulum pattern of body motion found in eight-legged crabs demonstrates that this energy-reducing mechanism is not restricted to birds and mammals (69). Gravitational potential and forward kinetic energy of the center of mass fluctuate 180° out of phase and are exchanged much like an egg rolling end over end or an inverted pendulum (103). Maximum possible walking speeds (u) can be estimated from a simple inverted pendulum model using leg length (L^S), where

$$u < \sqrt{g \cdot L^S} \quad (12-10)$$

and g represents acceleration due to gravity (10). In crabs, energy exchange when vaulting over relatively stiff legs can conserve 50% of the energy that must otherwise be produced by muscle (69). Data do not support the use of this mechanism in cockroaches, but obviously more insects need to be examined (207, 208). Energy exchange needs further study in invertebrate locomotion. Exchange is not restricted to the body and may occur between more than gravitational and forward kinetic energy components (for example, exchange may occur between lateral and gravitational components).

Running and Spring-Mass Models

$$k_{\text{rel}} = (F_{\text{vert}}/m \cdot g) / (\Delta L^S / L^S) = k^S n \quad (12-11)$$

In cockroaches and faster moving crabs, gravitational potential energy and forward kinetic energy fluctuate in phase similar to that of a bouncing ball. As the animal's body comes down on three or four legs, it is decelerated in the horizontal direction, while vertical force increases. The body is then accelerated forward and upward (that is, vertical force decreases). The pattern is repeated for the next set of legs. The body or center of mass attains its lowest position at midstance, much like we do when we run. In fact, the ground reaction force pattern for two-, four-, six-, and eight-legged animals can be fundamentally similar, despite the variation in morphology (69, 103, 207, 208, 248). All can run or bounce. Running humans, trotting dogs, cockroaches, and sideways running crabs can move their bodies by producing alternating propulsive forces. Two legs in a trotting quadrupedal mammal, three legs in an insect, and four legs in a crab can act as one leg does in a biped during ground contact. The center of mass of the animal undergoes repeated accelerations and decelerations with each step, even when traveling at a constant average velocity. Cockroaches and crabs do not necessarily show an aerial phase during the bouncing gait. These results suggest that a running gait should be redefined to include a complete dynamic description rather than depending on a single variable, such as an aerial phase. McMahon et al. (373) have shown that an aerial phase is not a requirement for the definition of a bouncing or running gait in humans. Gravitational potential energy and forward kinetic energy fluctuate in phase in humans running with bent knees and no aerial phase, like Groucho Marx.

Further evidence that multilegged invertebrates may use a running or bouncing gait equivalent to those of mammals comes from the examination of stride frequency. In quadrupedal mammals, stride frequency increases with speed in a trot. At higher speeds, quadrupeds switch to a gallop, where stride frequency increases only slightly but longer strides are taken to go faster. Ghost crabs (69) and cockroaches (207) show this trot-gallop transition with respect to stride frequency. Given the limited data, speed and stride frequency of the trot-gallop transition scale remarkably well for four-, six-, and eight-legged runners. A crab and a mouse of the same mass change from a trot to a gallop at the same speed and stride frequency, despite extreme differences in locomotor design (72, 191).

The model that best explains the running motion is a mass (the body) sitting on top of a virtual spring (the legs), where the relative stiffness of all legs acting as one virtual spring (k_{rel}) is calculated as follows:

where F_{vert} is the vertical ground reaction force of the virtual spring at midstance, ΔL^S is the compression of the leg spring, L^S is the length of the uncompressed leg spring, k^S is the relative individual leg stiffness, and n is the number of legs used in a step (67, 71, 372). Surprisingly, the k^S values of a running cockroach and a crab are remarkably similar to that found in trotting dogs, running birds, and bouncing kangaroo rats ($k^S \sim 10$) (71). The greater number of legs used in a step by six- and eight-legged trotters results in a greater virtual spring stiffness compared to two- and four-legged animals. The greater virtual spring stiffness produces a smaller compression of the virtual leg (which may be essential for small animals with crouched postures because large oscillations would result in contact with the ground) and a higher stride frequency. The relatively higher stride frequency may be possible because of the lower weight of each leg in a multilegged animal. Compared to legged vertebrates, arthropods distribute a similar force among a larger number of legs, enabling them to reduce the weight of an individual leg.

Design of Legs. Hughes (288, 289) proposed a simple model for the function of insect legs: legs could function as levers or inclined struts, depending on the direction of the ground reaction force vector. A leg functions as a strut if the ground reaction force vector is directed back toward the joint. If a significant horizontal accelerating force is observed, then the leg functions as a lever in the horizontal direction. Hughes and Mill (289) reported that the first leg of cockroaches functions as a lever, whereas the second and third legs function as inclined struts.

The data underscore the diversity of leg function in arthropods. Three-dimensional ground reaction forces for the legs of standing and slow walking spiders differ depending on the leg measured (68). Cruse (120) demonstrated that pro-, meso-, and metathoracic legs in a walking stick each generate a distinct ground reaction force pattern. Harris and Ghiradella (245) estimated the magnitude of vertical force and the direction of total force at the tarsus of each leg in crickets. Vertical force patterns are distinct in the second and third legs. Legs 4 and 5 of rock lobsters walking under water produce unique force patterns (115, 124): leg 4 appears to control movement, whereas leg 5 functions as a strut. In crayfish, leg 3 exerts the largest vertical force, whereas leg 4 produces most of the propulsive force (327).

Cruse (120) showed that the first and second legs of

stick insects act as levers or inclined struts, depending on the direction considered. Investigation of cockroach leg function (197) has also led to the conclusion that a strut–lever model alone is insufficient. Whole-body dynamics common to two-, four-, six-, and eight-legged runners can be produced by different numbers of legs that vary in orientation with respect to the body, generate unique ground reaction force patterns, but combine to function as one leg of a biped.

At a constant average speed, hexapedal runners generate a unique ground reaction force with each pair of legs (197). By contrast, each leg of a trotting quadrupedal mammal produces nearly the same force pattern during a step (9). A deceleration in the horizontal direction is followed by an acceleration, as predicted by a spring-mass model. The same pattern is found for the legs of trotting quadrupedal robots (421). Insects are not like quadrupeds with an additional set of legs. The first leg in cockroaches decelerates the center of mass in the horizontal direction during the complete stance phase, whereas the third leg is used to accelerate the body. The second leg produces a deceleration followed by an acceleration, much like legs in bipedal runners and quadrupedal trotters. Vertical force peaks for each leg are equal in magnitude, and significant lateral forces are generated. The sum of the leg forces in cockroaches produces a pattern consistent with a spring-mass model and similar to the whole-body, ground reaction force patterns of two- and four-legged runners.

Variation in the leg force patterns of insects coupled with their sprawled leg position results in the peak ground reaction forces being oriented toward the coxal joints (or hip equivalent) which articulate with the body. This arrangement can minimize joint moments and muscle forces (197). Legs of animals may not generate vertically directed ground reaction forces that result in large moments about the hip, as they do in some legged robots. Legs also do not operate under the horizontal, “zero-foot force” criterion used in the design of many-legged robots (491). Legs or “feet” push against one another in arthropods. Surprisingly, production of these horizontal and lateral forces associated with most of the mechanical energy generated during locomotion can actually reduce total muscle force by directing the ground reaction force vectors axially along the legs and through the leg joints. Locomotion with a sprawled posture, as seen in amphibians, reptiles, and arthropods, does not necessarily result in large moments around joints or large muscle forces. This is consistent with the finding that the minimum metabolic costs of transport in species that differ in posture can be similar (192, 193, 266).

Static vs. Dynamic Stability

Most six- and eight-legged arthropods use an irregular alternating tripod or tetrapod gait at most speeds such that at least three legs are on the ground at any time during locomotion. The legs of arthropods generally radiate outward, providing a wide base of support. It has been suggested that the morphology of the limbs provides stability against such disturbances as wind and uneven terrain. Alexander (10) has suggested that an insect such as the cockroach is so close to the ground that it must always have three legs in contact with the surface or it would fall to the ground before taking the next step. Hughes (288) stated that the six-legged condition is the “end-product of evolution” because the animal can always be statically stable (that is, at least three legs on the ground, with the center of mass within the triangle of support). Several robots have been designed with a quasi-static gait criterion that seems very similar to insect locomotion. The center of mass moves smoothly and is contained within a triangle or quadrilateral of support.

The advantages of a high static stability design (that is, a wide base of support and a low center of mass) at slow speeds in arthropods do not appear to preclude dynamic effects (465). Results from studies of six- and eight-legged runners (69, 197, 207, 208) provide strong evidence that dynamic stability cannot be ignored in fast, maneuverable, multilegged runners. Dynamic effects have not been incorporated in the design of most multilegged robots which remain slow and lack maneuverability (56, 63, 419, 445, 446, but see 420–421). The stability margin (that is, the minimum distance from the center of mass to the base of support) decreases linearly with speed and becomes negative at the highest speeds (that is, statically unstable where the center of mass lies outside of the base of support) (465). Crabs and cockroaches can use a running or bouncing gait that is dynamically similar to trotting in quadrupeds and running in bipeds (69, 71, 191, 207). Ghost crabs show a trot–gallop transition (69, 72). At these very high galloping speeds, ghost crabs propel themselves with two legs on the trailing side of the body as they leap into the air (69, 83). The American cockroach can run quadrupedally and bipedally at high speeds (208). Ants show aerial phases (535). These gaits demand dynamic stability. An animal can be dynamically unstable even when it has its center of mass within its base of support. In cockroaches and crabs, ground reaction forces create moments about the center of mass that cause pitching and rolling of the body. The resultant force of all legs or center of pressure is not directed through the center of mass

throughout the stride. The resultant force vector along with inertia could create a moment that would cause the animal to flip over. The animal remains dynamically stable because a force in one direction at one instant is later compensated by a force from another direction. Dynamic behavior, which uses kinetic energy to bridge gaps of instability, in conjunction with a highly statically stable sprawled posture allows rapid and highly maneuverable locomotor performance.

Jumping

Invertebrates can jump and jackknife to impressive heights. Fleas and grasshoppers can make jumps of 50 times their body length (50, 431). The take-off velocity (u_o) of a vertical jump is a function of jump energy (E_j) (48) and body mass (m):

$$u_o = (2E_j / m)^{0.5} \quad (12-12)$$

The theoretical height attained *in vacuo* (h_{vac} , no air resistance) is dependent on the takeoff velocity or jump energy and acceleration due to gravity:

$$h_{vac} = E_j / (m \cdot g) = u_o^2 / (2g) \quad (12-13)$$

Jump range (L_j) is a function of the angle of takeoff (ϕ):

$$L_j = u_o^2 \sin 2\phi / g \quad (12-14)$$

Body Size. Small animals could jump nearly as high as large animals if it were not for air resistance. The force (F_j)-time relationships required to attain a given jumping speed are approximated by the following:

$$u_o^2 = F_j \cdot 2d / m = u_o \cdot 2d / t \quad (12-15)$$

where d is the distance over which the acceleration is applied (a function of leg length) and t is the time between leg extension and takeoff, assuming a constant force production. As body mass decreases, the relative force available to move that mass increases. If we assume geometric similarity among small and large animals, area scales with body mass^{2/3}. Since this scaling may also apply to the cross-sectional area of muscles, small animals should be able to generate greater muscle forces relative to body mass than large animals ($F_j \propto m^{2/3}$). If the force per cross-sectional area is similar in small and large animals, then a small animal will be capable of higher accelerations because acceleration equals force divided by mass. However, small animals with their short legs cannot develop these accelerations over long takeoff distances ($d \propto m^{1/3}$ if geometrically similar). The result is that both large and small animals should be able to attain similar takeoff speeds and jump to the same height. Given a maximal

jump energy to mass ratio of 20 J/kg, jump height will not exceed 2 m (50).

Contrary to the aforementioned prediction, small animals cannot jump as high or far as large animals because mechanical power output is limited and drag becomes important (51). The shorter legs of small animals demand that relatively greater force be produced in a shorter time period. If power increases with a decrease in length such that power output $= d^{-1.5}$, then muscles in small animals could produce the energy necessary for high jumps given the muscle mass available. However, the problem is that muscle cannot deliver that energy in such a brief time period. The power must be amplified over a thousandfold by energy storage mechanisms (213). In addition to the force-time limitations of the takeoff, drag will reduce the height invertebrates can jump.

Ontogenetic scaling of jump performance in locusts does not follow geometric similarity (320). Discontinuities in scaling relationships are apparent between adults and juveniles. All juveniles attain similar maximum takeoff velocities and jump distances, whereas adults attain twice the velocity, possibly assisting in the initiation of flight. Legs tend to get longer and more slender as animals grow (319). The inherent deformability of long, slender legs may allow them to function as flexible springs, storing energy for the jump.

Drag. Small bodies encounter relatively higher drag forces than larger ones. Since drag force increases with the square of velocity, height attained in the upward phase of the jump is reduced (50). Jump height efficiency (h_{air} / h_{vac} , where h_{air} is the height attained in air) declines with decreasing body size, as shown by comparing fleas, fruit flies, and locusts (52). Aerodynamic drag is definitely important for small insects. For a given amount of specific energy, a 0.5 mg flea has only half the jump height efficiency, and therefore can jump only half the height, of a 0.5 g locust.

Below an Re of 1,000–2,000, the drag coefficient of streamlined bodies of all shapes may rise because viscous forces become more important. Drag becomes proportional to gross diameter, and streamlining has less effect. In general, small insects can decrease drag by decreasing their length until they approximate a sphere and reducing their frontal area to mass ratio by increasing body density. At an Re of 500–2,000, flies and bees have relatively short, blunt bodies.

Larger jumping insects operate at Re of 1,500–2,000, where shape and attitude change could minimize the drag coefficient (50). Moths, dragonflies, and locusts show streamlined, fusiform bodies. Even though a jumper may have a streamlined body, it may not be

able to control its orientation to minimize drag. Locusts appear to have some control of body attitude on takeoff, but after takeoff body attitude can change, resulting in rotation (418).

Wings add significantly to drag, but legs have much less of an effect. Not surprisingly, *aptery* (winglessness) occurs in the smallest jumping species. Small insects, such as some jumping fleas and flying fruit flies, fold their legs to reduce viscous drag, whereas others extend their legs, increasing drag but possibly adding stability.

Species. In the smallest jumpers, such as fleas, the takeoff distance is short so that high accelerations must be generated (on the order of 200 g) to attain the heights of larger animals (53). The short time available means that musculoskeletal power output must be increased significantly. Since the takeoff time is less than 1 ms, direct muscle contraction cannot provide the power output. Muscles cannot contract this rapidly. Instead, the flea uses a catapult system and stores energy in elastic material (*resilin*).

Click beetles have a very unusual mechanism for jumping (180): they jackknife into the air from their backs. They can jump 30 cm into the air, which requires an acceleration of 400 g. A peg prevents the movement of segments as the jump muscle builds force. When the peg slips, the stored energy allows the front half of the body to spring upward and a click is heard. Jumps are less efficient than in legged animals because 40%–50% of the energy is lost in rotation of the body.

Maggots weighing only 17 mg have been shown to explosively jump as high as 7 cm by accelerating to 86 g (352). Soft-body, hydraulic, legless forms are not precluded from performing high-speed locomotion.

Growth has a significant effect on jumping in locusts (214, 417, 418). At the beginning of the molt cycle, jumping range is low and increases to a maximum 2–5 days into each instar. After a maximum is attained, jump range decreases before the next molt (417). The result is a series of continuous parabolic changes in jump range separated by molts. Early larval instars, however, cannot jump as far as adults.

Flying

Invertebrates fly by gliding, soaring, hovering, and flapping wings. For an animal to fly, aerodynamic forces must balance against gravity and drag. Forward thrust must equal drag and the vertical force (lift) must support body weight. These forces are generated by wings that beat, twist, rotate, peel, clap, or fling. The blade element theory of propellers has been used to study gliding, soaring, and flapping flight (167). However, this theory ignores the existence of vortices related

to lift generation. Circulation around airfoils, helicopter, and vortex theories have been employed in the study of insect hovering and flapping flight because, as in swimming, unsteady forces appear to be important (169, 170). Present analyses take advantage of the spectrum of aerodynamic mechanisms available and do not simply focus on the use of steady vs. unsteady approaches (449). Although the use of these aerodynamic approaches has advanced, and will continue to advance, the field considerably, further rigorous experimentation is needed to visualize the flow necessary to reconstruct wakes of free flying insects to better understand wing and stroke forces (147, 156).

Aerodynamics of Wings and Bodies

Wings

Drag on the fixed wings of aircraft results from skin friction (viscous shear stress), pressure (or form), and induced drag (D_{ind}). Profile drag (D_{pro}) represents the sum of friction and pressure drag on the wings. Induced drag is associated with the wing's production of lift and represents the energy lost in the vortex wake. Total drag (D) on the wing is expressed as follows:

$$D = D_{pro} + D_{ind} \quad (12-16)$$

Drag coefficients measured for insect wings in wind tunnels include both components. The minimum drag coefficient (C_D , see equation 12-1) for bumblebee and fruit fly wings (0.1–0.3 at Re 1,200–200) due primarily to profile drag is about two to three times the value of a flat plate oriented parallel to flow (156). As Re is decreased, wings are less effective in generating lift but less sensitive to changes in their angle of attack. Drag coefficients increase relative to lift as Re decreases. The maximum possible lift coefficient decreases with an increase in Re. The most favorable drag to lift coefficient ratios shift to higher angles of attack at low Re. At the low Re of the fruit fly wing, the lift coefficient does not decrease even at angles of attack of 25°, where stalling normally occurs. Lift coefficients remain constant from a 20° to a 50° angle of attack. Stall-resistant features must be operating (484). The smallest insects (Re ≤ 20) have wings that look like drumsticks trimmed with two rows of fine bristles. These fliers may actually row around in the air like water beetles, using a drag-based instead of a lift-based mechanism (390).

The maximum lift coefficient (C_{Lmax}) in insects ranges from 0.6 (Re = 1,500) in bumblebees to 1.1 (Re = 4,000) in locusts. For a given wing, C_{Lmax} decreases with an increase in Re (390). This decrease may be caused by lower circulation around the wing resulting from reduced formation of leading edge bub-

bles due to the frequency of vortex shedding (168). One seemingly paradoxical finding is that the maximum lift coefficient measured on real wings at appropriate Re values can be less than the mean lift coefficient determined from kinematic records of flight, where average lift and drag coefficients are calculated along the wing at each phase throughout a wingbeat using a blade element analysis. Mean lift coefficients calculated from this quasi-steady aerodynamics approach nearly always exceed 1. This important finding suggests that quasi-steady aerodynamics is insufficient to explain insect forward flight and hovering (157, 170). Unsteady effects must be considered because quasi-steady aerodynamics ignores the effects of wake vorticity and the acceleration and deceleration of the wing.

Body Drag and Lift

Drag on the body of an insect is termed parasite drag. Parasite drag is a force that acts parallel to the airflow on the body. As in swimming, drag is a function of area, speed squared, and a drag coefficient (see equation 12–1). Body drag coefficients in insects fall between streamlined flow and fully separated flow. In bumblebees and other species, body drag coefficients decrease with increasing Re (157). Drag does not increase in proportion to the square of the air speed in flies, locusts, and moths. Drag coefficients also decrease with a reduced body angle of attack. Because body angle decreases with increased speed, parasite drag is reduced. Most importantly, the ratio of body drag to weight is small for flying insects; drag minimization may not be very important (485).

Body lift in insects is only a small fraction of body weight (156). Body lift represents 8%–14% in honeybees, 3% in cockchafer beetles, 4% in dipterans, and 10% in moths. Legs of honeybees have been shown to increase body lift by 24% (391).

Traditionally, comparative biomechanists and physiologists have somewhat arbitrarily divided flying into groups consisting of gliders, hoverers, and flappers. An insect flier can move from one to the other in a more or less continuous fashion within milliseconds. Yet, this categorization allows the elucidation of the important mechanisms involved in flight.

Gliding. If we assume that a gliding insect uses its wing as an airfoil, then we can use blade element theory to determine the aerodynamic forces involved (9, 10). If we also assume that the glider is in equilibrium with its body weight, is not accelerating, and has a relatively small gliding angle, then body weight ($m \cdot g$) should nearly equal lift and gliding speed (u):

$$u = (2N / (\rho C_L))^{0.5} \quad (12-17)$$

where N is wing loading [equal to $(m \cdot g) / A$, where A is the plan area] and C_L is the lift coefficient (10). High wing loadings are best suited for faster gliding. Gliders can also go faster by increasing the lift coefficient with a change in the angle of attack of their wings (but not above a maximum of about 1–1.5).

If a glider wishes to stay airborne as long as possible, it must minimize sinking speed ($u \sin \theta$);

$$u \sin \theta = u D / (m \cdot g) \quad (12-18)$$

where θ is the glide angle relative to the horizontal and D is drag. To minimize sinking speed, parasite, profile, and induced drag can be reduced (10).

To travel as far as possible for a given loss of height, small gliding angles must be used. The minimum glide angle (θ_{\min}) is a function of the drag coefficient (C_D) and the aspect ratio (AR , the length of the span to the mean cord);

$$\sin \theta_{\min} = (C_D / AR)^{0.5} \quad (12-19)$$

Large aspect ratios allow gliding at shallower angles of attack (10).

Species

The wings of gliding locusts operate at an Re of 5,000 and have a maximum lift coefficient of about 1.2 (299). The minimum speed below which gliding is impossible is 2.9 m/s. Wing loading in locusts is relatively low (6.5 N/m^2), the parasite drag coefficient relatively high (1.0), and the minimum gliding angle steep (30°). Therefore, locusts should glide very slowly and for short distances, sinking rapidly, relative to other gliders, such as vultures (9). The butterfly *Pieris brassicae* has a very low wing loading for its size (0.7 N/m^2), and its minimum glide speed is only 1 m/s (268).

Body Mass

If gliders are geometrically similar, then wing area would be proportional to $\text{mass}^{2/3}$, wing loading to $\text{mass}^{1/3}$, and gliding speed to $\text{mass}^{1/6}$ (10). Although there is enormous variation, large animals tend to have higher wing loadings and, therefore, higher minimum glide speeds. The small size of locusts prevents them from traveling against a heavy wind, and they cannot glide as far as larger animals, such as birds, for a given loss of height. Also, most profile drag on airfoils is friction drag, which decreases with an increase in Re; therefore, larger animals can glide at shallower angles and travel farther than small animals.

Forward Flapping Flight. Surprisingly few studies have been conducted on free, forward flapping flight in insects. Complete aerodynamic analyses have proved extremely difficult. Studies on tethered flight have pro-

vided significant advances. However, several investigations have shown that the wing beat frequency and speed of tethered flight can differ from free flight (156, 334).

A common description of flight wing kinematics involves chordwise sections operating roughly horizontal to the ground on the downstroke and tilted slightly up at the leading edge on the upstroke (9). The resultant lift and drag act upward and forward on the downstroke because the wing has a positive angle of attack. Thrust and vertical force are, therefore, developed on the downstroke. On the upstroke, the principal force is drag because the wing has a small angle of attack. Tethered locusts show dynamics consistent with this description. They fly with a positive angle on the downstroke and a slightly negative one on the upstroke (299). Only a small downward lift on the upstroke may occur because the forewing is pleated and the aerodynamics unusual.

Studies on free-flying bumblebees (156, 157) and flies (390) show that thrust production on the downstroke is only one of the possible scenarios. A difference in wingbeat frequency or wing stroke amplitude could change the relative flapping velocity of wings and, therefore, the magnitude and direction of force production. The advance ratio (J , the inverse of the reduced frequency parameter) represents the ratio between flight velocity and mean wing flapping velocity:

$$J = u / (2 L_{\text{amp}} \phi L^W) \quad (12-20)$$

where u is flight velocity, L_{amp} is stroke amplitude, ϕ is wingbeat frequency, and L^W is wing length (156). In general, advance ratios are relatively low in insects with asynchronous flight muscles [for example, 0.13 in bumblebee workers (156)] and greater than 0.9 in some butterflies (152). In particular, small insects at low Re have high wing drag. Very high wingbeat frequencies are used to generate a small lift component. An increase in advance ratio would result in stroke forces becoming increasingly asymmetrical. The relative velocity of the downstroke becomes greater than the upstroke. The downstroke tends to become more horizontal and the upstroke more vertical. As advance ratio increases, lift forces tend to predominate on the downstroke and thrust on the upstroke.

Hoverflies, flies, and locusts increase wingbeat frequency with speed, but data show considerable variation (156). The increase in frequency is somewhat offset for free-flying insects because they tend to decrease stroke amplitude with speed. In bumblebees, wingbeat frequency and stroke amplitude do not change with speed (156). In both cases, the advance ratio tends to increase with speed. Perhaps more im-

portantly, bumblebees and some flies change the angle of attack of their wings gradually to increase thrust by generating a force asymmetry between the downstroke and the upstroke. Changing the angle of attack and increasing the advance ratio results in vertical forces that increase in magnitude on the downstroke and horizontal forces that increase on the upstroke with an increase in speed. During the upstroke, the wing path forms a loop that is directed upward and posteriorly. High lift and little thrust are generated on the downstroke, whereas little lift and higher thrust are generated on the upstroke (390).

Quasi-steady analysis of forward flight assumes that instantaneous forces on flapping wings correspond to those of steady motion at the same instantaneous velocity. Weis-Fogh and Jensen (509) concluded that the quasi-steady assumptions were adequate for flying locusts. However, steady effects dominate when advance ratios are relatively high (or the reduced frequency parameter is low) (167). Some insects use low advance ratios. Cloupeau et al. (117) showed, by measuring cyclic forces, that the quasi-steady approach was insufficient for locusts. Dudley and Ellington (157) showed that the minimum required lift coefficient always exceeded 1 in flying bumblebees, whereas measurements of wings in wind tunnels never exceeded 0.8 in steady flow. Unsteady aerodynamics has been deemed important in flies and butterflies using the same reasoning (153, 178, but see 155).

Vortex theory, which considers unsteady effects by examining puffs of air that form rings, offers refined estimates of induced velocity and power not possible with a quasi-steady approach. Because of assumptions about wake geometry, however, vortex theory may be less appropriate for the low advance ratios found for some flying insects (157). Azuma and Watanabe (27) have applied a local circulation method to the forward flight of dragonflies that accounted for first-order unsteady effects, an improvement over actuator-disk-based estimates. Brodsky (81) has shown that useful force, as seen in vortices, is produced continuously throughout the wingbeat in tethered butterflies. Grodnitsky and Morozov (237) have argued, from laser dust flow visualization experiments of tethered flight, that insects produce a series of sequential independent vortex rings.

If corrections to vortex wakes are insufficient, then high-lift mechanisms must be postulated. Mechanisms that may explain an increased lift in forward flight include a delayed stall, where transient high lift on aerofoils occurs at angles of attack greater than the stalling angle; opposite wing interaction; wing translation with increasing angle of attack; and wing rotation at either end of the beat to produce circulation (449).

Hovering

Wing Kinematics

Most insects hover by beating their wings in a horizontal stroke plane (167). The wings have a small positive angle of attack on the downstroke and upstroke. For the upstroke, the wings turn upside down so that the anterior edge remains the leading edge and lift is produced by both strokes (9, 10). Many of these fliers hover with their body axis held more vertically with respect to the ground. Other insects, such as true hoverflies and dragonflies, hover with their bodies more horizontal, beating their wings up and down through relatively small angles. They use a more inclined stroke plane. True hoverflies beat their wings in a plane oriented 30°–40° from the horizontal. Dragonflies have an inclined stroke of as much as 60° and produce very small forces on the upstroke. The downstroke forces support their mass. The butterfly *Pieris brassicae* beats its wings in a nearly vertical stroke plane. Little force is produced on the upstroke. The vertical force results from pressure drag on the wings during the downstroke (at Re-2,800). A drag-based mechanism has been predicted in small insects, but some which have a horizontal stroke plane (for example, the fruit fly at Re of only 200) may be better characterized by a circulatory lift mechanism.

Unsteady Effects

In hovering, as in forward flapping flight, the mean lift coefficients determined on each section of a wing over a complete cycle of wing movements are equal to or greater than the maximum steady-state lift coefficient, so unsteady flight mechanisms must be considered. Lift coefficients of 6 for dragonflies, 2–3 for hoverflies, and 3 for a tiny wasp are far greater than the values of near 1 predicted by steady effects in the same Re range (10).

One of the best understood of the unsteady effects is the “clap and fling” mechanism discovered by Weis-Fogh (507). The left and right wings of the tiny wasps studied (*Encarsia*) clap together at the top of the upstroke. The anterior edges separate first on the downstroke and air flows around the wings, setting up a circulation that increases lift. Butterflies appear to use a clap and fling on takeoff and must rely on vortex patterns created by wing movements (167, 459, 460).

In general, the lift forces used in hovering flight are circulatory in nature and not virtual or added mass in origin (169). Circulation is attributable to the vorticity in leading edge separation bubbles, which may form on the wings at low Re (but see 237). In hoverers using an inclined stroke, a delayed stall may be used to maintain the enhanced circulation and lift. Hoverflies

and dragonflies use circulation created by the vorticity of rotation at the high angular velocities of the wings. Dragonflies beat their fore- and hindwings a half-cycle out of phase with each other. Instantaneous circulation must lag substantially behind the quasi-steady value because of the Wagner effect (that is, vorticity shed into the wake causes the instantaneous circulation to change more slowly). *Drosophila* wings can undergo a late rotation about the trailing edge during stroke reversal, which can generate large amounts of lift (530, 531). Using a model dynamically scaled to Re, Dickinson (146) demonstrated how simple wing flips in small insects could be a source of force production. Augmentation in lift is very sensitive to subtle changes in kinematics, which suggests remarkable maneuverability with potentially sophisticated control.

The major problem for all theories of hovering is the uncertainty of circulation profiles. The pulsed actuator disc and vortex models of wing action in hovering offer a framework for estimating mean force, induced velocity, and induced power (170, 449). Although conceptually important, the induced power calculated from vortex theory differs by less than 20% from previous estimates from momentum theory for hovering with a horizontal stroke plane.

Comparison of Locomotor Dynamics

The diversity of locomotor mechanisms among invertebrates is impressive. Yet, there are common variables which can lead to hypotheses concerning muscle function and its energetic support. As discussed in the previous sub-sections on MECHANISMS OF LOCOMOTION, most modes of locomotion involve cyclic movements of propulsors. Appendages, bodies, feet, and cavities operate rhythmically at a measurable frequency, the *propulsive* or *cycle frequency*. During one cycle time, the animal moves forward a given distance, the cycle distance. Frequency and distance traveled per cycle determine the speed of locomotion. The frequency of a propulsor can be correlated with the rate of musculoskeletal contraction and relaxation since the muscles and their attachments must also function cyclically. The distance traveled per cycle can be correlated with the extent of musculoskeletal shortening and lengthening. Both correlations depend on the musculoskeletal unit's nature, its orientation with respect to the rest of the skeleton, and the nature of the propulsive unit.

Sustaining a particular locomotor speed demands mechanical power output from the propulsive unit (Fig. 12.1A). This mechanical power output must be related to musculoskeletal mechanical power output. Since muscles and apodemes convert chemical energy to mechanical energy for whole-animal locomotion through

the transfer of energy to segments of the propulsive unit, the rate, duration, and degree of musculoskeletal contraction and relaxation can be correlated with the muscle's metabolic support systems (Fig. 12.1B).

Although examining speed, frequency, and mechanical power output for diverse species is valuable, the functions reported herein are simply relationships of the most general sort. Unfortunately, data on the relevant variables for all regressions to follow are sometimes unavailable for whole groups of animals, limited to a particular species within a group, or simply not comparable (that is, the sample is insufficient and not random). Data are also not independent; therefore, grouping species and phylogeny must be considered for particular comparisons (see the chapter by Bennett in this *Handbook*). Finally, the almost irresistible temptation to place undue significance on scaling exponents must be avoided. Because diversity and variation are high, correlations are low and different regression models (for example, major axis and reduced major axis) give different values for scaling functions.

Speed. The speed of locomotion can be an important performance variable for physiologists, behaviorists, and ecologists. Speed is expected to vary with size, species, body temperature, and mode of locomotion.

Ideally, one would like to know an animal's preferred speed (selected most often by the animal), maximum sustainable speed, speed at minimum energy cost per time and distance, and maximum possible speed. Data on invertebrate locomotion from a wide variety of sources are not ideal however, since in most studies other issues were being addressed. Given the available data on invertebrates, the separation of recorded speeds into these categories does not allow any additional generalizations to be made compared to simply grouping all of the speeds. In general, speeds tend to be closer to maximum sustainable than to maximum.

It is important to note that generalizations concerning speed are biased by the nonrandom distribution of species that have been studied and that size, species, temperature, and mode of locomotion are not always independent. Future investigators interested in speed should collect data that include size (mass and length), body temperature, and phylogeny.

Size

Depending on the mode of locomotion, most similarity models predict that speed increases with length and mass. The present data show little dependence of flight speed on body mass over three orders of magnitude in body mass (Table 12.1; Fig. 12.3). Jumping takeoff

TABLE 12.1. *Scaling of Speed as a Function of Body Mass*

Mode	Name (Taxonomic Group)	Mass Range (kg)	Speed (m·s ⁻¹) = a m ^b		r	n	P
			b (S.E.)	log a (S.E.)			
Running	All	0.0000062–0.255	0.089 (0.064)	-0.62 (0.20)	0.20	51	0.17
	Insects	0.0000062–0.0052	0.099 (0.090)	-0.58 (0.318)	0.20	32	0.28
	Crustaceans	0.00192–0.225	0.160 (0.253)	-0.40 (0.492)	0.21	11	0.54
Jumping	Insects	0.0000004–0.003	0.069 (0.060)	0.50 (0.30)	0.38	10	0.29
Swimming	All	0.00000017–0.50	0.094 (0.036)	-0.74 (0.126)	0.48	25	0.02
	Crustaceans (walking on bottom)	0.0092–0.50	0.283 (0.141)	-0.57 (0.212)	0.67	7	0.10
	Crustaceans (swimming)	0.00000017–0.046	0.112 (0.055)	-0.66 (0.213)	0.46	18	0.05
Flying	All	0.0000015–0.002	0.049 (0.046)	0.55 (0.19)	0.17	39	0.30
	Flies, bees (Diptera, Hymenoptera)	0.0000015–0.00054	0.133 (0.044)	1.07 (0.204)	0.61	18	0.008
	Butterflies, moths (Lepidoptera)	0.000024–0.0011	0.337 (0.088)	1.41 (0.325)	0.72	16	0.002

speeds and running speeds show a similar independence. Swimming speed increases over seven orders of magnitude in body mass, but the predicted variation between the smallest and largest species is only 4.5-fold. When individual taxonomic groups are examined, speed tends to show a greater increase with body mass (Fig. 12.3B). Bees, flies, mosquitoes, and lepidopterans show significant regressions (Table 12.1). Running and swimming crustaceans show greater positive regression slopes than all swimmers and runners, but the relationships are weak. Insufficient data are available to scale crawling and jet propulsion speeds.

Mode of Locomotion

The best predictor of speed is the mode of locomotion used (Fig. 12.3). One gram fliers travel at speeds 20 times as fast as those used by runners or swimmers of the same mass. Jumping takeoff speeds are only slightly lower than flight speeds. The fastest runners can move at speeds of slow fliers and jumpers. Jet propulsion is the fastest mode of aquatic locomotion in invertebrates and can be similar to the speeds of jumpers, slow fliers, and fast runners; however, many of the jetters are quite large. Invertebrate swimmers and runners move at similar speeds. Aquatic runners move as fast as slow terrestrial runners but may not sustain the speeds of the fastest runners on land. Runners and swimmers move 20–100 times faster than crawlers. Fliers fly at speeds 2,500 times faster than snails crawl. The fastest recorded crawlers, such as caterpillars, move at rates similar to those of slow runners, walkers, and swimmers.

Temperature

Runners and swimmers attain similar speeds, despite swimmers operating at lower temperatures (0°–23°C) than runners (22°–42°C). A correction in temperature for the sake of comparison is questionable because swimmers that operate at temperatures of runners do not show significantly higher speeds than species at lower temperatures and it is unlikely that animals acclimated to swimming at near 0°C could increase speed by 16-fold at 40°C (that is, performance typically decreases at the highest temperatures within a species). Correcting the speed of runners to the higher body temperatures of many fliers using a Q_{10} of 2 makes the differences in speed among fliers and runners smaller but appears insufficient to explain the 20-fold higher speeds of fliers.

An increase in speed with temperature is very apparent within species of crawlers, swimmers, and runners. For example, ants change speeds by 15-fold over a 30°C temperature range, from 0.44 cm/s at 8°C to 6.6 cm/s at 38°C (435). The speed of rolling dung balls is

directly proportional to thoracic temperature in dung beetles (40).

Species

Insects show the greatest range of speeds (0.03–8 m/s). Fliers are the fastest members of the taxon next to jumpers. Bees, flies, and mosquitoes are faster than some butterflies. The fastest cockroaches and beetles run at speeds similar to jumping and slow flying. Beetles and other species that swim move at speeds comparable to walkers and runners. Crawling insect larvae are the slowest members of the group. The fastest crustaceans are those that jet (for instance, shrimp) and those that sprint on land (for instance, crabs), but these speeds cannot be sustained for more than several seconds. Cephalopod molluscs (for instance, squid) and some bivalves (for instance, scallops) that employ jet propulsion move at speeds 500 times that of gastropod crawlers in the same taxon. Jellyfish jet propulsors move at speeds of slow swimmers.

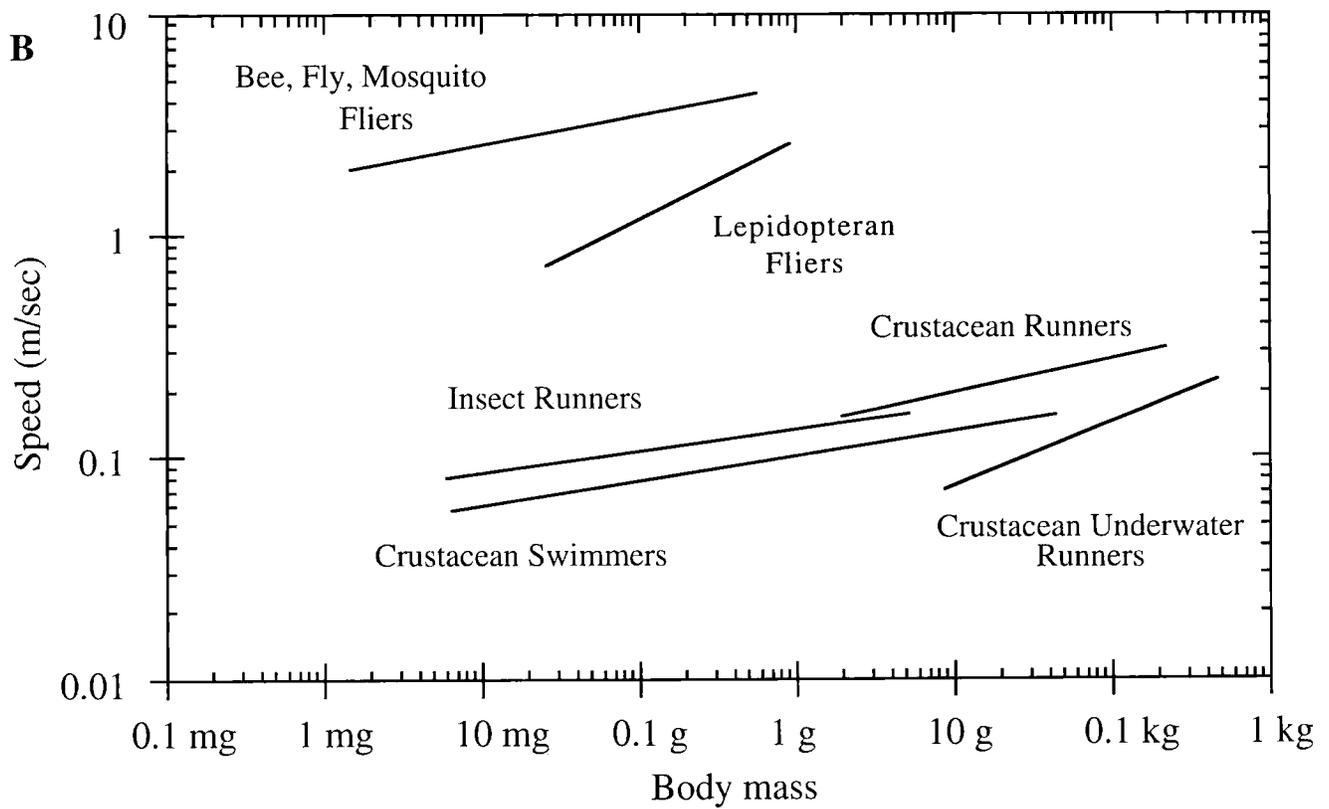
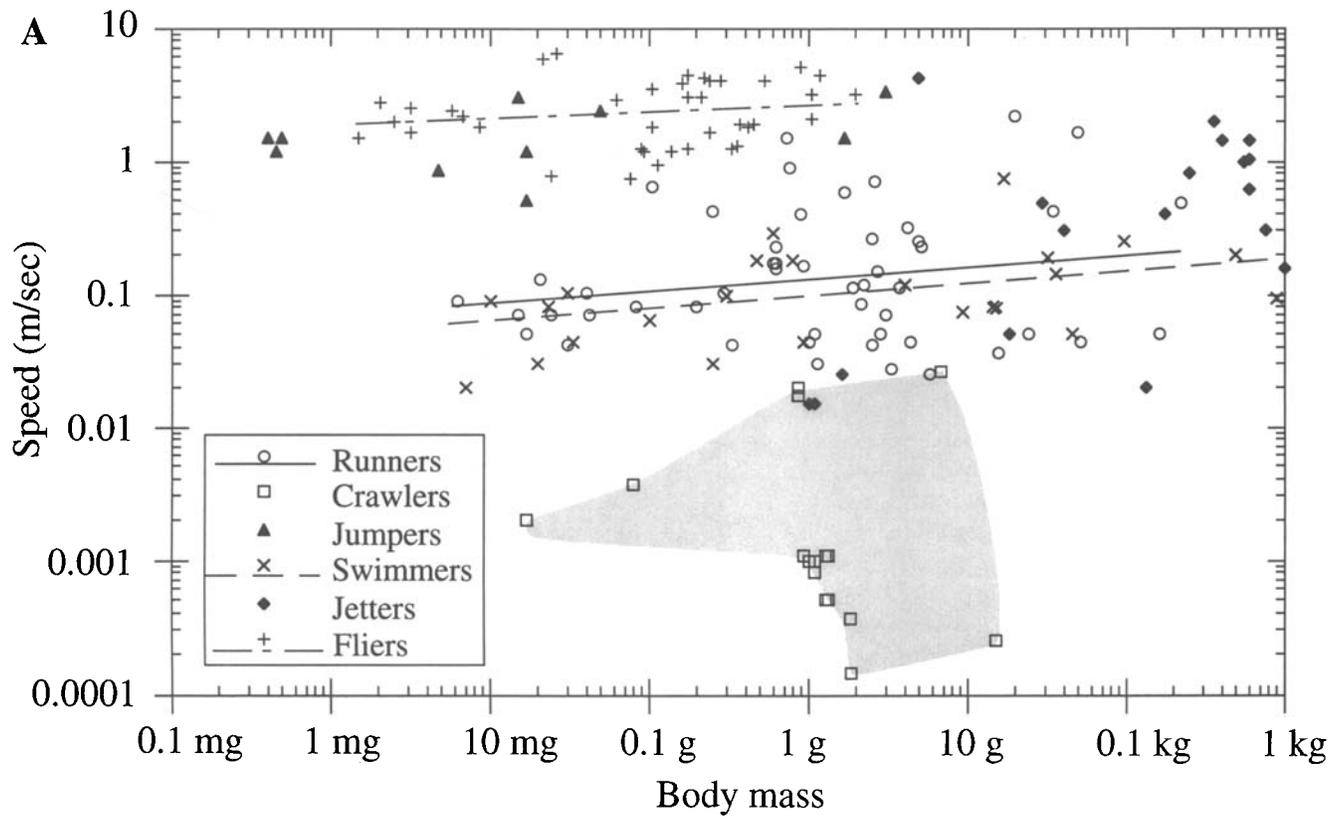
Frequency. The frequency of the propulsive unit used in locomotion (wingbeat, stride, or wave frequency) is an important variable in determining speed and directly affects the capacity of the musculoskeletal system powering movement. Frequency is expected to vary with speed, size, species, body temperature, and mode of locomotion. Just as for speed, one would like data for an animal's preferred frequency, maximum sustainable frequency, frequency at minimum energy cost per time and distance, and maximum possible frequency. Data on the propulsor frequencies used in invertebrate locomotion, with the exception of flying, are surprisingly sparse.

Speed

Speed can be increased by the distance traveled per cycle or frequency so that increases in the frequency of the propulsive unit are expected but not obligatory. Numerous studies on terrestrial arthropods, such as stick insects, beetles, cockroaches, crickets, and crabs, show that stride frequency increases with speed. However, ghost crabs and cockroaches eventually attain a speed at which stride frequency no longer increases with speed, and the animals run faster by taking longer strides (191). Free flight in a wind tunnel by bumblebees shows no dependence of wingbeat frequency on speed (156). Bumblebees travel farther for each wing stroke as speed increases.

Size

Allometric predictions of the frequencies used in invertebrate locomotion vary but follow a trend of decreasing frequency with an increase in body mass,



where frequency = $m^{-1/6}$ to $-1/3$. The majority of the data are from flying insects (see ref. 235 and original sources). The wingbeat frequencies of hovering euglossine bees, bumblebees, sphinx moths, and saturnid moths have been reported to decrease with an increase in body mass (96, 102). The present analysis also finds the negative scaling of wingbeat frequency in beetles, flies, crane flies, white flies, and aphids (Table 12.2; Fig. 12.4). Mosquitoes, flower flies, and dragonflies show similar trends but with considerable variation. An exception to this trend is found in the noctuid and geometrid moths, where wingbeat frequency increases with an increase in body mass because the relative wing area decreases in large animals (101).

Stride frequency at the proposed trot–gallop transition in terrestrial arthropods decreases with body mass and tends to follow the same function describing mammalian tetrapods (249). Recorded data for all invertebrate runners are limited and variable but tend to scale to a negative power of body mass (Table 12.2).

Invertebrate swimmers scale with an exponent similar to that of runners and fliers (Table 12.2; Fig. 12.4). In swimming water beetles, frequency decreases with body length as $L^{-0.39}$ (approximately $m^{-0.14}$) (389).

Mode of Locomotion

Fliers use the highest propulsive frequencies when the effects of body mass are removed. One gram bees beat their wings over 15 times the rate of leg movements used by runners of the same mass (Fig. 12.4B). By contrast, 1 g butterflies appear to have wingbeat frequencies comparable to the stride frequencies of runners. Runners may employ higher frequencies than swimmers, but the data remain too variable to draw a conclusion. Swimming water beetles use rowing frequencies comparable to walkers and runners (389). Jet propulsors use the low frequencies predicted for swimmers of a large mass. Data are insufficient for a comparison of crawlers.

Species

Insects have the greatest range of frequencies, from 1,000 Hz in the smallest species (448) to 2.5 Hz in caterpillars (97). Fliers using asynchronous flight muscles have wingbeat frequencies that tend to be greater than synchronous fliers. Synchronous flight muscles were once thought to have a 100 Hz limit, but Josephson (313) found that synchronous muscles in a cicada operate at 550 Hz. One gram bees beat their wings at three times the rate of sphinx moths, at five times the frequency of dragonflies, and at 13 times the rate of butterflies of the same mass. The smallest fliers, wasps, aphids, and white flies, have one-fifth the wingbeat frequency predicted for asynchronous fliers of a similar mass. In general, wingbeat frequency is correlated with wing length and shape. Longer wings and lower wing loadings (that is, greater wing area for a similar weight) allow generation of more lift per cycle and, therefore, are associated with lower wingbeat frequencies (96).

Temperature

The highest frequencies are found in species that have the highest body temperature; however, temperature is also correlated with species and mode of locomotion. In many flying insects (Odonata, Lepidoptera, Diptera, and Hymenoptera), wingbeat frequency increases with temperature but has a relatively low Q_{10} (1.0–1.4) (366). Foraging and hovering bumblebees show no relationship between body and thoracic temperatures and wingbeat frequency (306). Cockroaches increase stride frequency by 50% for a 10°C increase in temperature when running at the same speed (209).

Mechanical Power Output. The data on whole-body mechanical power output are the most scarce of all of the data on the important common mechanical variables. Yet, its measurement provides the link between muscles

FIG. 12.3. Speed as a function of body mass. A: Speeds of fliers, jumpers, runners, jetters, swimmers, and crawlers. Shown are maximum speeds available from the literature. Some speeds are reported as truly maximum. The majority are near maximum aerobic speed (speed at which maximal oxygen consumption is attained). Many are preferred speeds. For jumpers, take-off speeds shown. The shaded area bounds the speed of crawlers. Data include runners (22, 41, 69, 83, 134, 136, 181, 199, 201, 202, 207, 208, 212, 259, 261, 263–266, 278, 290, 343–347, 383, 392, 413, 458, 523), crawlers (97, 145, 277, 292, 353), jumpers (11, 48, 53, 179, 180, 282, 352), swimmers (7, 65, 114, 119, 184, 241, 276, 278, 280, 290, 293, 328, 369, 386, 409, 466, 468, 482, 511), jetters (106, 127, 128, 130, 132, 294, 338, 395, 398, 399, 473, 474, 475), and fliers (45, 152, 155, 156, 173, 273, 367). (Ref. 158 published after submission of figures.) B: Regression lines of major taxonomic groups (Table 12.1). Data to generate regressions include insect runners (41, 136, 181, 207, 208, 212, 259, 263, 266, 343–347, 383, 392, 458); crustacean runners (69, 83, 199, 202, 261, 264, 265, 278, 290, 523); crustacean swimmers (7, 119, 184, 241, 276, 280, 293, 328, 369, 386, 409, 466, 468, 482); crustacean underwater runners (114, 276, 278, 280, 290); bee, fly, and mosquito fliers (156, 173, 273); and lepidopteran fliers (152, 155). Note the change in speed axis from A.

TABLE 12.2. *Scaling of Cycle Frequency as a Function of Body Mass*

Mode	Name (Taxonomic Group)	Mass Range (kg)	Frequency (cycles · s ⁻¹) = a m ^b		r	n	P
			b (S.E.)	log a (S.E.)			
Running	All	0.00004–0.050	-0.247 (0.150)	0.144 (0.424)	0.50	10	0.14
Swimming	All	0.000023–0.50	-0.227 (0.074)	0.055 (0.226)	0.81	7	0.028
Flying	Bees, flies, mosquitoes (Hymenoptera, Diptera)	0.000001–0.0016	-0.163 (0.021)	1.555 (0.092)	0.66	77	<0.001
	Dragonflies (Anisoptera)	0.000061–0.0012	-0.077 (0.065)	1.16 (0.225)	0.22	30	0.25
	Beetles (Coleoptera)	0.00011–0.00026	-0.290 (0.084)	0.81 (0.276)	0.79	9	0.011
	Flies (Diptera)	0.000002–0.00028	-0.188 (0.040)	1.336 (0.191)	0.75	19	<0.001
	Flower flies (Diptera)	0.000013–0.00015	-0.085 (0.092)	1.834 (0.405)	0.24	16	0.371
	Crane flies (Diptera)	0.0000012–0.000069	-0.109 (0.032)	1.224 (0.152)	0.89	5	0.042
	Mosquitoes (Diptera)	0.000001–0.000067	-0.319 (0.187)	0.858 (1.022)	0.57	8	0.138
	Bees, wasps (Hymenoptera)	0.000021–0.0016	-0.170 (0.044)	1.568 (0.165)	0.56	34	0.001
	Aphids and white flies (Homoptera)	0.00000033–0.0000007	-0.256 (0.046)	0.366 (0.316)	0.90	9	0.001
	Butterflies (Lepidoptera)	0.000024–0.00339	-0.139 (0.099)	0.563 (0.375)	0.28	25	0.175
	Sphinx moths (Lepidoptera)	0.00039–0.0034	-0.263 (0.108)	0.788 (0.315)	0.48	22	0.025
	Saturnid moths (Lepidoptera)	0.0002–0.0014	-0.225 (0.230)	0.547 (0.754)	0.25	16	0.344

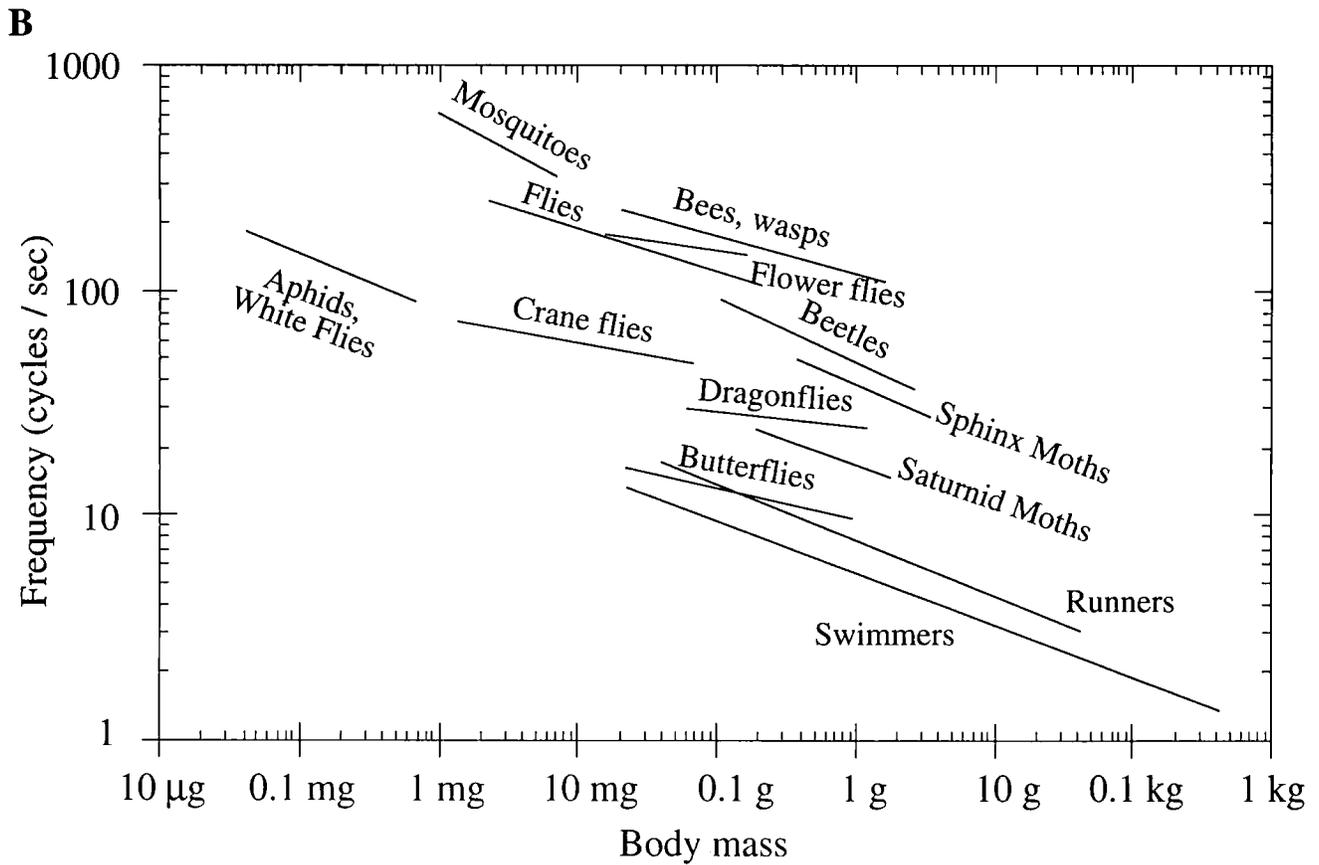
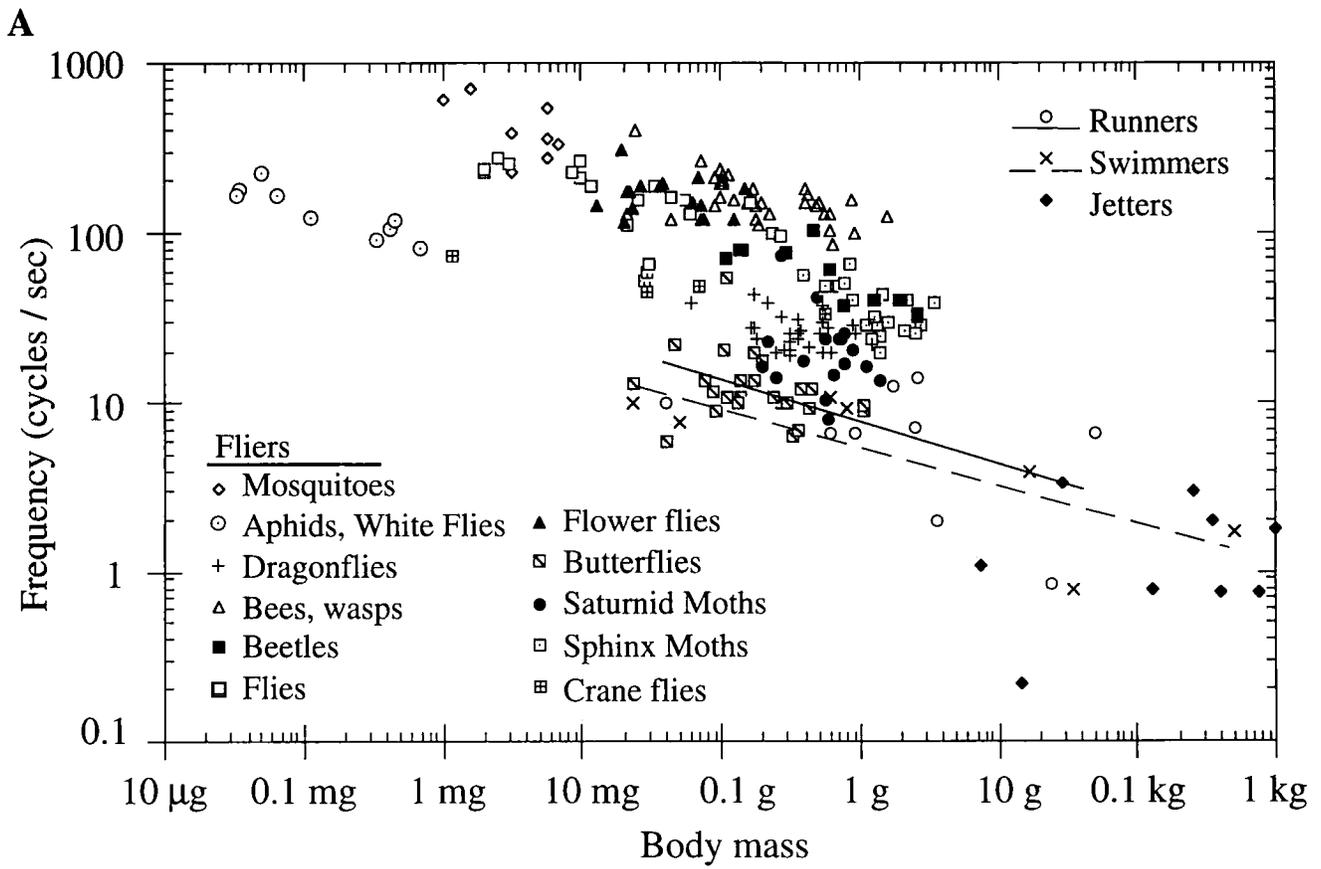
moving segments and segments moving the animal (Fig. 12.1A).

Speed

FLYING. Mechanical power output for insect flight is dependent on parasite, profile, induced, inertial, and center of mass powers (154, 157). Parasite power is the drag on the body times the forward airspeed. The

parasite drag force acting parallel to the airflow on the body is proportional to the square of the forward speed; therefore, parasite power should increase with forward velocity raised to the third power (154). Profile power is the friction and pressure drag on the wings times the relative velocity of the wing (157). Profile power is calculated at each instant of the wingbeat and summed for each consecutive spanwise section over the

FIG. 12.4. Cycle frequency as a function of body mass. A: Cycle frequency of fliers, runners, jettlers, and swimmers. Frequencies shown are the maximum available from the literature. Some frequencies are reported as truly maximum. The majority are preferred speeds. Data include runners (22, 69, 134, 207, 208, 212, 261); swimmers (7, 65, 114, 290, 409); jettlers (29, 106, 127, 140, 338, 473, 495); and fliers such as mosquitoes (84, 273, 366, 507), aphids, white flies (84, 524), dragonflies (84, 366, 367), bees, wasps (84, 96, 156, 171, 306, 366, 507), beetles (84, 507), flies (84, 273, 318, 366, 507, 524), flower flies (84, 318, 507), butterflies (84, 152, 507), saturnid moths (39, 84, 96, 507), sphinx moths (94, 96, 366, 507), and crane flies (84, 171, 366, 507). B: Regression lines of major taxonomic groups (Table 12.2). Note the change in cycle frequency axis from A.



whole length of the wing. The minimum profile drag coefficient for flying insects shows that skin friction is most important, with an additional component coming from pressure drag. Induced power is required for lift generation to impart downward momentum to the air to offset the effects of gravity. Induced power equals induced velocity times the weight of the insect less any lift forces (154). Induced velocity results from air traveling downward due to a pressure pulse. Less momentum needs to be provided by beating wings as speed increases; therefore, induced power is inversely proportional to forward velocity. Parasite, profile, and induced powers represent the useful work done on the environment and when summed together are termed aerodynamic power.

Inertial power is required to accelerate the mass and virtual or added mass of the wings. The inertial power of the wing is equal to the wingbeat frequency, moment of inertia of the wing, and added mass, and the square of the angular velocity attained by the wings (154). If the kinetic energy of oscillating wings can be stored in musculo-skeletal structures, then the inertial power may be small. Dickinson and Lighton (148) have argued that energy storage greater than 10% would not further reduce the power requirements of flight in species where inertial and aerodynamic powers are similar because the energy recovered by elastic storage is exactly offset by a loss in aerodynamic power savings. Inertial power involved in body movements relative to the center of mass is often assumed to be small.

Finally, center of mass power is related to oscillations of the body that result in the fluctuations in kinetic and potential energy of the center of mass and is analogous to that described for terrestrial locomotion (154).

The total mechanical power output for flight is predicted to yield a U-shaped curve because profile and parasite power requirements increase with speed but induced power decreases with speed. At most speeds, the parasite power component is very small in magnitude. Contrary to predictions, free forward flight in bumblebees and many flying vertebrates does not result in a U-shaped curve (157). Total mechanical power output does not change with speed. Estimates of inertial power do not change with speed and represent the major power expenditure if no elastic strain energy storage is present. The mechanical power output in migrating moths increases exponentially at high speeds (152). Since the moth operates at fairly high advance ratios, forward airspeed has a greater influence on the flow over the wings. The increase in power output is primarily due to an increase in profile power.

SWIMMING. The determinants of mechanical power output for swimming are in many respects comparable

to those for flight. The components include the power associated with overcoming body drag, appendage or propulsor movement, and inertial and added-mass forces. In contrast to flight, most of the power output in swimming is generally considered to be parasite power (P_{para}). At low Re, power (P) output is determined as follows:

$$P = k_{\text{vis}} \mu L^5 u^2 \quad (12-21)$$

but side-to-side movements that cancel in some organisms can raise this estimate by 50-fold (525). At high Re, power output should increase with approximately the cube of swimming velocity:

$$P_{\text{para}} = \rho C_D u^3 \quad (12-22)$$

where C_D is the parasite drag coefficient. Power output in swimming copepods (385), euphasids (467), water beetles (387), water boatmen (65), walking lobsters (61), and jetting squid (398) increases exceptionally with speed, though not necessarily to the third power. At high Re, studies have shown that inertial and added-mass effects become the most significant in swimming (64, 307). As in flight, reported values of mechanical power output as they relate to muscle remain uncertain due to the possible contribution of elastic strain energy storage in swimming invertebrates.

RUNNING. Paradoxically, the average mechanical energy output of constant speed terrestrial locomotion is zero since in most animals drag is negligible (203). The relevant mechanical power output is instead dependent upon the repeated fluctuations in energy over a stride. Accelerations and decelerations of the body or center of mass are referred to as external power and the rocking of the body and the swinging of the limbs relative to the center of mass is termed internal power (70, 192). The magnitude of external power output is taken to equal the sum of the positive increases in gravitational potential energy and vertical, lateral, and horizontal kinetic energies of the center of mass during a stride multiplied by stride frequency. The magnitude of internal power output is equal to the sum of the gravitational potential energy, kinetic energy of rotation, and kinetic energy of translation of each segment in the animal relative to the center of mass during a stride multiplied by stride frequency, but the problems of reciprocal movements and energy transfer make the estimate difficult (70).

Only three studies have determined the mechanical energy output for running in invertebrates. For two species of cockroach (207, 208) and one crab (69), estimates of total mechanical power output increase linearly with speed at low and intermediate speeds. In each species, the increase in power with speed results primarily from increases in the rate of external energy

and, more specifically, in horizontal kinetic energy. Vertical kinetic energy changes are small and the rate of gravitational potential energy generation is relatively constant with speed. At the fastest speeds attained by the American cockroach (1.5 m/s, 50 body lengths/s), mechanical power output increases exponentially with speed because the fleet insect must overcome substantial parasite drag (203). The internal energy of the legs has been estimated to contribute significantly (30%) to the power output at the fastest speeds used by ghost crabs (69).

Energy exchange, transfer, and storage can play an important role in terrestrial locomotion. For example, in ghost crabs, energy exchange using an inverted pendulum mechanism during walking can conserve as much as 50% of the mechanical energy that must otherwise be produced by muscle (69). Future research needs to be directed toward energy generation and absorption by segments (see later under Muscle–Organism Level). Energy may be stored in springs, but the contribution of elastic strain energy storage in running, as in other modes of locomotion, is uncertain.

Size

The scaling of mechanical power output has been elusive for at least three reasons. First, measurement

of mechanical power output is challenging. Besides the technical difficulties, the contribution of elastic strain energy storage can potentially confound scaling if one attempts to relate energy to muscle function: if no storage of elastic strain energy is assumed (zero storage) and storage is present, then mechanical power output by the muscle is overestimated; if complete storage of elastic strain energy is assumed (perfect storage) and no storage is present, then mechanical power output by the muscle is underestimated. Second, selection of an appropriate speed for comparison of animals that differ in mass and mode of locomotion is troublesome and can affect scaling. The scaling of mechanical power output at maximum speed, maximum sustainable speed, or some equivalent speed may differ. Third, insufficient data are available.

FLYING. The data for hovering flight give us our best guess about the scaling of mechanical power output. Aerodynamic power output tends to be directly proportional to body mass in hovering insects (507). Therefore, relative to their mass (that is, on a mass-specific basis), small and large fliers expend about the same amount of mechanical energy per unit time (Fig. 12.5). Mass-specific aerodynamic power scales to $m^{0.08}$ in hovering sphinx moths (94) and to nearly the same exponent in euglossine bees (99). Mass-specific aerody-

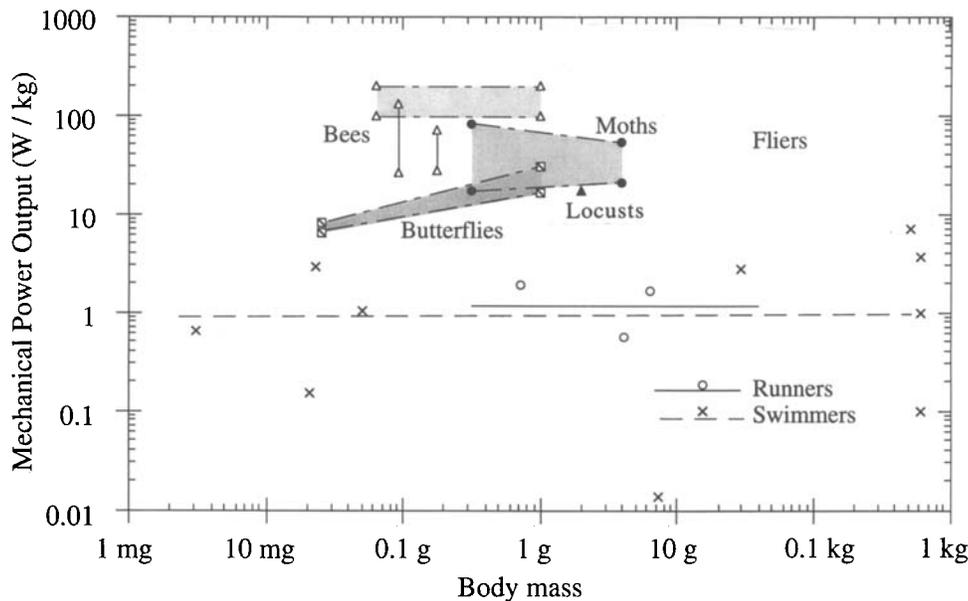


FIG. 12.5. Whole-animal mass-specific mechanical power output as a function of body mass. Shaded areas and connected points represent the range of possible values for fliers, assuming 0 (upper bound) and 100% (lower bound) elastic storage. Speeds selected are the maximum available from the literature. Some speeds are reported as truly maximum. Many are preferred speeds. Data include insects (207, 208) and crabs (69) for terrestrial locomotion; crustaceans (385, 467), insects (65, 3890), jellyfish (140), and molluscs (127, 397, 398) for aquatic locomotion; and insects (94, 102, 153, 173, 299, 504) for aerial locomotion.

dynamic power increases in butterflies with mass ($m^{0.26}$) (153). Casey (95) has argued that mass-specific inertial power may even scale to $m^{0.4}$ based on both mechanical and metabolic estimations, but unless the amount of elastic strain energy storage is known, uncertainty exists. If elastic strain energy storage varies with body mass, then scaling exponents for use in muscle power output estimates could change significantly.

SWIMMING. Hydrodynamic power output may also scale in direct proportion to body mass; however, the present variability in the data set is large. An equivalent speed for comparison is difficult to select, and few species have been examined. However, the mass-specific mechanical power output of a 3 mg copepod and a 0.5 kg squid are both near 1 W/kg (Fig. 12.5). Mass-specific power output in swimming water beetles is relatively independent of body mass ($m^{-0.10}$) (389).

RUNNING. Mass-specific power output for running cockroaches and crabs compared at maximum speeds shows no trend with mass, but more data are needed. If mass-specific power output of runners is compared at an equivalent speed, then a positive scaling could result, as in butterflies. Surprisingly, the amount of mechanical energy used to move a 1 kg body mass 1 m is the same for six- and eight-legged runners that differ in mass (that is, the slope of the mass-specific mechanical power vs. speed function). Even more remarkably, this mechanical energy of transport (see Fig. 12.14G) is about 1–10 J/kg/m in birds and mammals and differs little for over five orders of magnitude in body mass (191, 192).

Mode of Locomotion

The mechanical power output of insect flight exceeds that of swimming and running by as much as 100-fold. Values for flight range from 8 to 200 W/kg, depending on assumptions concerning storage of elastic strain energy (Fig. 12.5). Euglossine bees expend about 100 W/kg (perfect elastic storage) to 200 W/kg (zero elastic storage) to hover (102), whereas the lowest values for forward flying butterflies are comparable to the highest values for runners and swimmers. The highest mechanical power outputs for terrestrial locomotion in invertebrates determined thus far approach about 2 W/kg at speeds of near 1.5 m/s (208). Values as high as 2.95 W/kg have been reported in swimming insects when added-mass effects are included [for example, water boatman (65)]. No difference between the power outputs of running and swimming can be discerned.

Species

Euglossine bees have the highest recorded mechanical power outputs if one assumes no storage of elastic

strain energy (Fig. 12.5). Rates for moths can be less than half those for bees. Butterflies have the lowest power outputs of the fliers studied to date. Estimates would be even lower if Dudley (152) had not shown that the total mechanical power output of forward flight in palatable butterflies is increased by 43% on average when the erratic trajectories of the body are included. Variation in mechanical power output is considerable in cephalopod molluscs. The highest values are found in the squid *Illex* and the lowest in *Nautilus* (397). Jellyfish jet propulsors have the lowest estimated mechanical power outputs (140).

Temperature

Few attempts have been made to determine if mechanical power output varies as a function of temperature across species or in a given species at a given speed. With the scant data set at hand, we find that species at low temperatures can have relatively high power outputs but that the highest power outputs are found in hot insect fliers. Certainly, rate functions are temperature-dependent; therefore, we would expect that frequencies may be affected so that examination of kinematics may provide clues. Full and Tullis (209) found that the kinematics of cockroach locomotion varies as a function of temperature. Legs are lifted higher at lower temperatures and body instability becomes obvious. Both of these changes may result in an increased mechanical power output at a given speed. The prediction at present is that mechanical power output at a given speed is temperature-dependent. This temperature dependence may be more significant at lower temperatures than at high. However, the dependence may be reduced by the possibility that faster fibers or muscles with greater power output are recruited as temperature is decreased (424). This is an important area for future research, requiring actual measurement of mechanical power output at different temperatures.

PRODUCTION OF LOCOMOTION: MUSCULOSKELETAL SYSTEMS

Examining how invertebrates locomote and quantifying common variables such as speed, frequency, and power output allows general predictions to be made concerning the structure and function of muscles and skeletons. Muscles of small animals operating at high frequencies most likely differ from those of large animals. Flight muscles generating high power outputs are expected to differ from leg muscles in insects. Muscles of fast moving invertebrates with jointed framework

skeletons are likely to differ from those of animals that move slowly with hydrostatic skeletons.

Studies of invertebrate muscle offer great promise in the search of how muscles power locomotion (315). Enormous variation among invertebrate species, within species, and even within the same muscle is present in both structural and functional components. Moreover, the opportunity exists for manipulation of these components at the genetic level (493). Also, the ease of use in experimentation with respect to stimulation, energy supply, and joint arrangements makes them ideal systems.

Linking even a “simple” invertebrate musculoskeletal system to the movement of a segment or whole body is still a challenge (Fig. 12.1B). Muscles perform in a variety of ways in the locomotion of invertebrates. In some cases, they are primarily force generators (near isometric contractions) used for stabilization and support of limbs and skeletons, allowing the possibility of spring-like function. In other cases, they function more as velocity generators for the rapid movement of limbs or body parts. Most often, muscles generate and absorb energy, operating with a combination of force and velocity of shortening or lengthening. Muscles act through their attachments to the skeleton, so geometry (that is, moment arms) and elastic strain energy storage must also be considered. Perhaps muscle can best be described as acting like a spring (that is, length-dependent), an independent and controlled force generator (that is, activation-dependent), and a dashpot (that is, velocity-dependent) (529). These functions can be explored only by examining a variety of levels of organization. I discuss muscle structure and function from the level of the cell to the organism to integrate musculoskeletal function with segment movement (Fig. 12.1B).

Filament, Sarcomere, and Muscle Level

The sarcomere is often stated to be the unit of function in muscle; however, many invertebrates do not possess muscle with well-defined sarcomeres. Many simply lack cross-striations (for example, musculoepithelial cell collections) or are transverse or obliquely striated (336, 337, 492). Perhaps a more fundamental unit of contraction is a myofibril cluster. Nevertheless, since more work is necessary to define the mechanical properties of non- or disorderly striated muscle (and this is an important area for the future), I emphasize the function of more well-defined invertebrate striated muscle involved in locomotion.

Several models of sarcomere function have been proposed based on the work of A. V. Hill, A. F. Huxley, and others. Sarcomere models (402, 450, 480, 481)

promise to bridge the gap between structure and function from the molecular to the organ level. Since the first attempts at such models must make simplifying assumptions, further development and tests are necessary. Because of their diversity, invertebrate locomotor muscle can and should serve as natural tests of muscle models. Several invertebrate components which show rich variation have not yet been considered in models but could lead to a greater understanding of muscle function in general.

Force Production. Muscle force production is closely linked to muscle morphology. Contemporary models provide a framework to link muscle function to molecular structure. Active force production depends on the number of cross-bridges available and the average cross-bridge force (480, 481). The number of cross-bridges available is a function of the number of myosin heads per unit length of myosin filament and the extent of overlap in thick and thin filaments. Maximal force of the sarcomere will occur when the number of myosin heads per unit length of myosin filament, the average cross-bridge force, and the length of the myosin filament (Fig. 12.6D) are maximized and the length of myosin devoid of cross-bridges (bare zone) is minimized.

The maximum isometric force developed by a muscle (F_o^M) depends on the force developed by a sarcomere and the number of sarcomeres in parallel. Therefore, the maximum force production of muscle is a function of cross-sectional area (A^M) and is often written as follows:

$$F_o^M/A^M = \sigma^M \quad (12-23)$$

where σ_o^M represents muscle stress.

The development of force in muscles is also a function of the angle of pennation of their fibers. If a muscle has fibers of length (L_o^M) at optimal filament overlap where maximum isometric force is attained, maximum stress (σ_o^M) and volume (V^M), then the cross-sectional area is V^M / L_o^M and the force is $V^M \sigma_o^M / L_o^M$ (11). If fibers attach at an angle α and the muscle is pennate, then the maximum force along the apodeme (F_A) or connective structure is calculated:

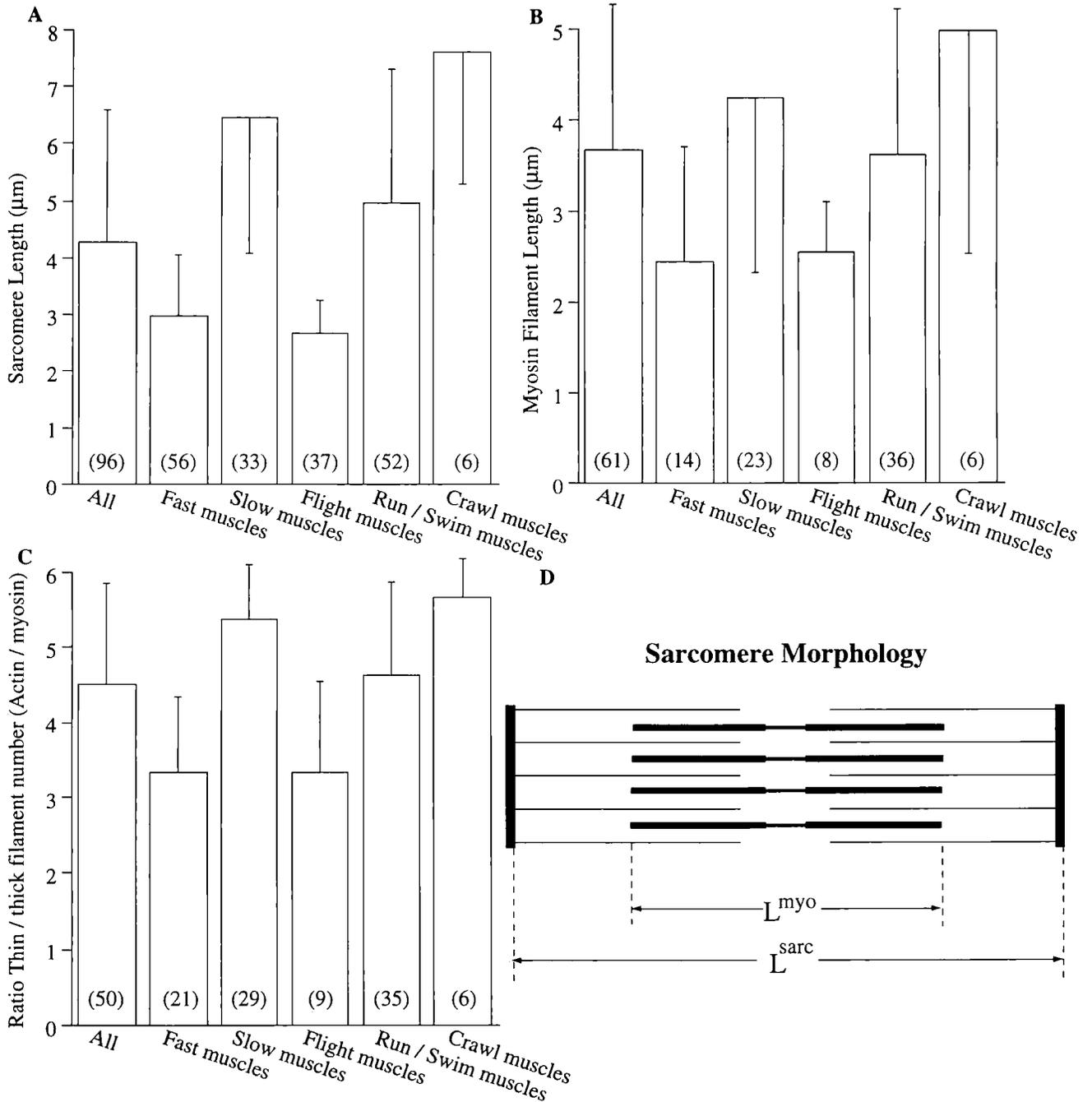
$$F_A = \sigma_o^M (V^M / L_o^M) \cos \alpha \quad (12-24)$$

The shape of active force–length curves (see force–length discussion later in this section) may differ between relatively fusiform (parallel-fibered) and pennate muscles. The slope of the active increment can be very steep at long lengths in pennate muscles (4). Length changes in fibers of pennate muscles are much greater at long lengths than at short lengths for a given change in whole-muscle length because the fibers become ori-

ented more parallel with the direction of length change. Therefore, $\cos \alpha$ is a function of muscle length. If fusiform and pennate muscles of the same volume are compared, then pennate muscle will exert a greater force because L_o^M will be much smaller and the cross-sectional area relatively greater. Using a pennate muscle can be equivalent to increasing mechanical advantage, but shorter fibers contract more slowly and move the apodeme or skeletal connection through a shorter distance.

Maximum Isometric Stress

Variation in the length of sarcomere structures can alter maximum stress. In general, muscle fibers with long myosin filaments (based on A-band measurements) tend to develop a greater maximum tension than those with short filaments (direct measurements of both in a variety of species are few; therefore, only a trend is seen statistically). Longer myosin filaments (L^{myo}) are found in longer sarcomeres (L^{sarc} ; for all



invertebrates $L^{myo} = 0.50 L^{sar} + 0.86$, where both values are reported; lengths are in micrometers; $n=43$, $P < 0.001$). Sarcomere lengths vary between and within species and even within the same muscle fiber. Variation in sarcomere length in arthropods is less within a muscle fiber than between fibers (308). However, in a crab leg, myosin length may even differ in the two halves of a single sarcomere (188). Sarcomere lengths for invertebrate locomotor muscles (mean = $4.3 \mu\text{m} \pm 2.3$ S.D.; Fig. 12.6A) are twice that of most vertebrates, as are the lengths of myosin filaments (mean = $3.7 \mu\text{m} \pm 1.6$ S.D.; Fig. 12.6B). Muscles categorized as slow (by function, histology, or histochemistry) and associated with greater isometric force development than faster muscles have longer sarcomeres, longer myosin filaments, and a greater ratio of actin to myosin filaments (Fig. 12.6A–C).

MODE OF LOCOMOTION. Crawlers have the longest sarcomeres, the longest myosin filaments, and the greatest number of actin to myosin filaments (Fig. 12.6A–C). Sarcomeres and filament lengths do not differ in runners and swimmers. Fliers have the shortest sarcomeres, the shortest myosin filaments, and the fewest number of actin to myosin filaments (Fig. 12.6A–C).

SPECIES. Values of maximum isometric stress range from 16 to 803 kN / m² or kPa (mean = 242 kN / m² \pm 286 S.D.; $n = 15$). In the cockroach leg (479) and the abdomen of lobsters (295), tension development is greatest in the slowest muscles.

BODY SIZE. Maximum isometric stress does not show any significant trend with body mass. Variation in isometric tension is on the order of 50-fold.

TEMPERATURE. Temperature has little effect on maximum isometric stress in invertebrate muscle (309). In 20 orthopteran flight muscles, maximum isometric stress varies by less than 5% for a change in temperature of 5°C. The largest changes are seen at the lowest temperatures. Stress tends to increase with temperature; however, in some species, it can actually decrease (309).

COMPONENT VARIATION. Maximum isometric force is often assumed to be proportional to the cross-sectional area of the muscle fiber. However, comparisons among species may be misleading since the number of myosin heads per myosin filament length and the proportion of muscle cross-section occupied by myofibrils are variable. Groups of myosin heads are called crowns, and each crown can contain four heads in insects compared with three heads in vertebrates (5). Moreover, myosin filament thickness can vary by twofold and is greatest in cells with the largest thin to thick filament ratios (286). Thin to thick filament ratios vary from less than 2:1 to 7:1 in invertebrate locomotor muscles (Fig. 12.6C). High thin to thick filament ratios are usually associated with long myosin filaments and greater force production. A greater number of actin filaments may reduce the stress on each individual filament (5). Considerable variation in the volume of sarcoplasmic reticulum (range 1%–40%; mean =

FIG. 12.6. Sarcomere morphometrics. Muscles were divided into fast and slow groups based on a variety of criteria, which included fiber type, enzyme level or activity, and contraction kinetics. In general, if a study designated a muscle as fast or slow, this characterization was used. All insect flight muscles were considered to be fast. All crawlers—larvae, worms, and nematodes—have slow muscles. Walking and swimming organisms have both fiber types. Bars represent ± 1 S.D. Numbers in parentheses are sample size. L^{myo} , myosin filament length; L^{sar} , length of a sarcomere. A: Sarcomere length. Data include insects such as locusts (48, 51, 285, 504), cockroaches (163, 185, 287, 296, 382, 415, 454, 479), water bugs (5, 25, 163), water beetles (162), katydids (5, 164), lepidopterans (89, 422), dragonflies (444), larvae (86, 88, 243, 401, 422), nymphs (87), flies (405, 434), and hemipterans (125); crustaceans such as lobsters (287, 295, 296, 415), crayfish (1, 415, 461, 528), crabs (188, 283, 476), and merostomatans such as horseshoe crabs (490); arachnids such as spiders (321, 436) and scorpions (26, 425); molluscs such as scallops (379) and cuttlefish (286); annelids such as worms (376, 462) and polychaetes (365); chaetognaths such as arrow worms (161); and coelenterates such as jellyfish (107, 439). B: Myosin filament length. Data include insects such as locusts (118, 285), cockroaches (5, 163, 239, 240, 287, 296, 415, 479), water bugs (5, 25, 163), water beetles (162), katydids (5, 164), lepidopterians (5, 513), dragonflies (444), larvae (86, 88, 243, 401), and nymphs (87, 90); crustaceans such as lobsters (295–297, 415), crayfish (415, 528), and crabs (188, 283, 476); arachnids such as spiders (321, 436); molluscs such as scallops (379) and cuttlefish (286); annelids such as worms (376, 462), and polychaetes (365); nematodes (426); and coelenterates such as jellyfish (107, 439). C: Ratio of thin/thick filament number. Data include insects such as locusts (118, 285), cockroaches (5, 239, 240, 287, 296, 415, 454, 479), water bugs (5, 25), katydids (5, 164), lepidopterians (89, 422, 513), dragonflies (444), larvae (86, 88, 243, 401, 422), nymphs (87, 90), and flies (405); crustaceans such as lobsters (287, 296, 415) and crabs (188, 283); arachnids such as spiders (436) and scorpions (26, 425); molluscs such as scallops (379) and cuttlefish (286); annelids (376, 462); nematodes (426); and coelenterates such as jellyfish (107). D: Sarcomere diagram shows designated lengths.

21% \pm 11.3% S.D.; $n = 13$) and mitochondria (range 3%–44%; mean = 21% \pm 16% S.D.; $n = 7$) are present in invertebrate locomotor muscle. A more appropriate comparison for questions concerning the contractile apparatus might be force per unit area of myofibrils (308). Models of sarcomeres or muscle do not generally consider variation in myosin, thin to thick filament ratio, and noncontractile material. This is an area for future research (402, 480).

PENNATION. Pennation may play an important role in invertebrate locomotion. Pennate muscle can develop over four times the force of parallel-fibered muscle of the same volume in the hindlegs of locusts (388). Perhaps more importantly, pennate muscle is less limited in its force development when enclosed in a rigid, confined space, such as an arthropod's leg. Parallel-fibered muscle swells when it contracts, which could restrict force development in a tubular space. Pennate muscle does not swell because the increase in α is compensated by the shortening of the fibers. The importance of pennation in invertebrate locomotion deserves more attention.

Force–Length

Active force production varies with the amount of filament overlap, sarcomere length, and therefore muscle fiber length.

SPECIES. Force–length curves for invertebrate locomotor muscle show considerable variation. Relaxed or passive invertebrate locomotor muscles vary in stiffness (242). The parallel-fibered insect flight muscle has a very high resting tension and is relatively stiff (5). The high stiffness could be the result of c-filaments that connect the myosin to the Z-disk (231, 470, 515, 533). The flight muscle can be damaged or broken by only a 5% stretch (349). Pennate leg muscles with longer isotropic bands (I-bands) have lower resting tensions (186). Resting tension in insects can be influenced by sustained evoked contractions and contractures induced by hormones in the presence or absence of neural stimulation (186). Relaxed crustacean leg muscles have a stiffness similar to the frog semitendinosus muscle if stretched slowly (415). Supercontracting muscle used in the body wall of some muscular hydrostats can be relatively compliant and is more similar to nonstriated (smooth) invertebrate and vertebrate muscle (243).

Active length–tension curves vary among species (Fig. 12.7). The most striking differences are seen when the flight muscle is compared to the body wall muscle of hydrostats that crawl. Flight muscle generates maximum isometric tension over a very narrow range of lengths (Fig. 12.7). In flight, asynchronous muscle undergoes very small length changes (2%–4%; Fig. 12.7; see also Fig. 12.8B at high frequency) as the sarcomeres

simply vibrate. By contrast, body wall musculature (helical, obliquely, and cross-striated) operates over a very large range of length changes corresponding with the considerable shape changes in these species. Blowfly larvae striated trunk muscles can generate 50% of their maximum tension at 52% and 150% of the resting length and can give supercontractions down to 22% of the muscle's resting length [Fig. 12.7; (243)]. Supercontracting muscles have a perforated, discontinuous Z-disk, allowing actin filaments to pass through the disk and interact with the myosin of adjacent sarcomeres (88). Synchronous flight muscles that cycle at lower frequencies than asynchronous muscles may have broader length–tension distributions than flight muscles that operate at higher frequencies (Fig. 12.7). The muscles of runners and swimmers that use their exoskeletons can develop substantial amounts of force at longer and shorter lengths compared to flight muscles but cannot generate force at the length changes seen in the body wall musculature of hydrostats. The striated muscles of appendages for these runners and swimmers can undergo length changes of 8%–40% and may not break even after stretches of 200%.

Force–Velocity Relationship. Force production is dependent on the velocity of contraction and is typically expressed in the form of the Hill equation (269). Shortening velocities decrease with an increase in isotonic force production. The force–velocity relationship for lengthening is less well defined (315).

Reported shortening velocities of invertebrate locomotor muscle vary by over 53-fold (range 0.3–16 lengths/s) (315, 349) depending on the slowest muscle of a hydrostat selected for inclusion. Maximum shortening velocity (u_{\max}^M) tends to be inversely proportional to sarcomere rest length and proportional to muscle length. Shortening velocity is proportional to the number of sarcomeres in series. A fiber with more short sarcomeres in series can contract more rapidly than one with fewer longer sarcomeres. Alternatively, the fiber with more sarcomeres can contract at comparable velocity but use a lower interfilamentary velocity. Faster contracting muscles tend to have short sarcomeres, whereas slower contracting ones have longer sarcomeres, longer myosin filaments, and higher ratios of thin to thick filaments associated with greater force production (Fig. 12.6).

Mode of Locomotion

Sarcomere lengths of flight muscles (mean = 2.7 μm) are consistent with their high rate of contraction (Fig. 12.4A) and are about half the length of swimming and running muscles of other invertebrates (Fig.

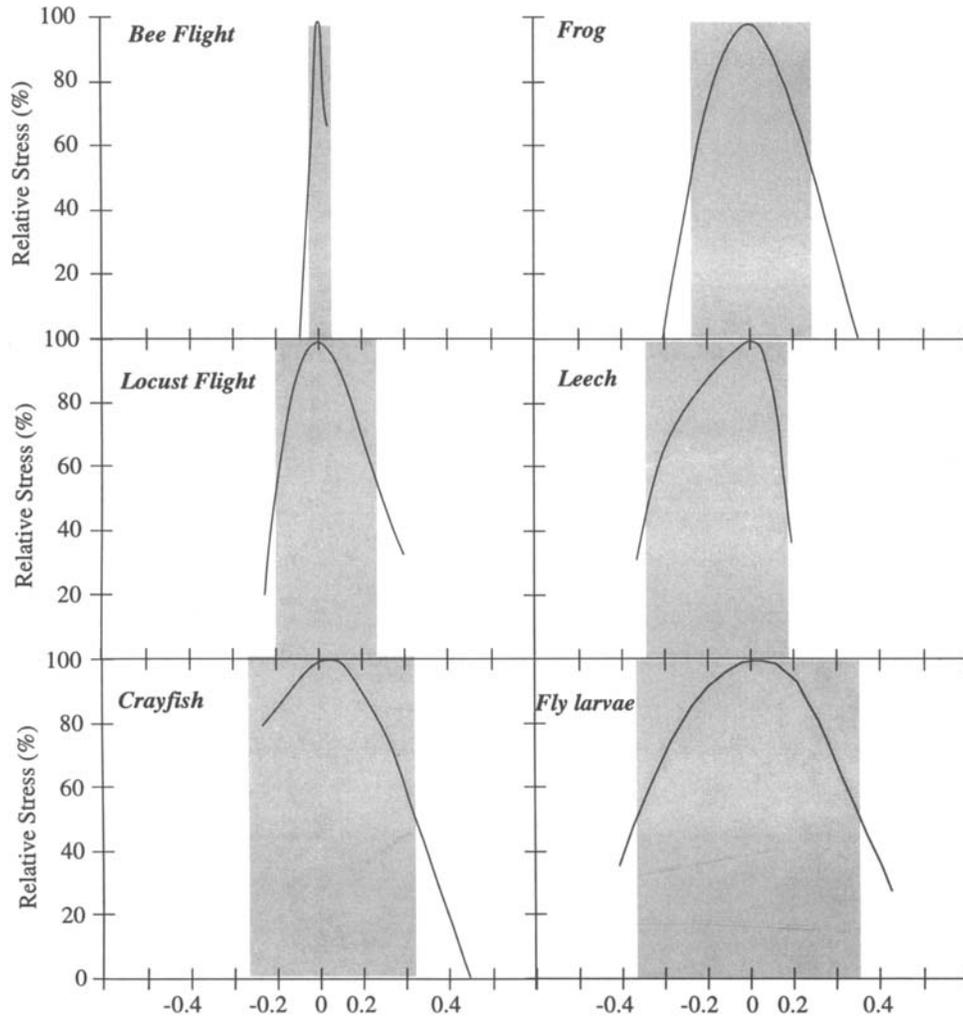


FIG. 12.7. Active length–tension or strain–stress curves of invertebrate muscles. Stress is normalized to peak isometric tension. Strain is normalized as a fraction of the length that gives peak isometric stress. Shaded areas represent strains that correspond to stresses above 50% maximal isometric stress. Data include bee flight (242), locust flight (353), crayfish (528), frog (271), leech (378), and fly larvae (243) muscles.

12.6A). Flight muscles have a mostly 3:1 ratio of thin to thick filaments, whereas other invertebrate muscles that generate larger forces have ratios of 4:1 to 7:1. Sarcomere lengths of crawlers are consistent with their slow rates of locomotion (Fig. 12.3A) and are 50% longer than those of runners and swimmers and 280% longer than those of fliers.

Body Size

Shortening velocity of invertebrate locomotor muscles increases with cycle frequency (ϕ) and decreases with body mass. Data from studies using the work-

loop method (Figs. 12.8, 12.9) show that strain rate at maximum power output increases by 16-fold with an 89-fold increase in muscle cycle frequency (strain rate in lengths / s, $\dot{u}^M = 0.34 \phi^{0.67}$; $r = 0.91$; see Fig. 12.8 for refs).

Species

Force–velocity curves have been constructed for a few invertebrate locomotor muscles (242, 310, 353, 354, 362). Locust, katydid, beetle, and scallop muscles show the characteristic hyperbolic shape, with force decreasing with an increase in velocity. Some of the

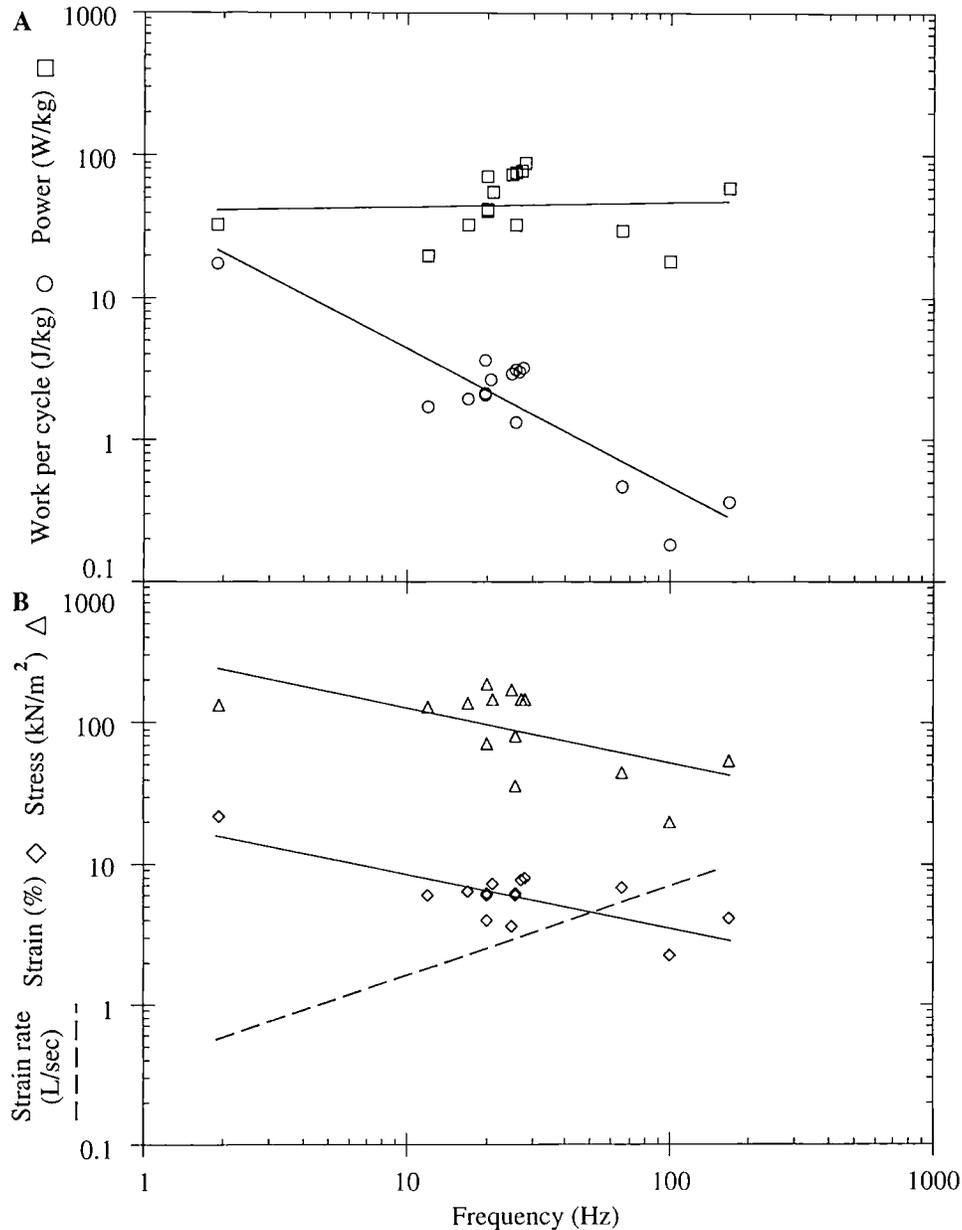


FIG. 12.8. Mechanical power output of invertebrate muscle and its determinants as a function of cycle frequency. Data are from isolated muscle studies using the work-loop method (Fig. 12.9) and come from unpublished data of Stevenson and Casey. *A*: Mass-specific mechanical power output and work per cycle. Gilmour and Ellington (223) have demonstrated values as high as 110 W/kg from asynchronous, glycerinated muscle fibers of bumblebees. *B*: Muscle stress, strain, and strain rate. Data include insects (312, 349, 380, 453), crustaceans (455), and molluscs (362).

curves available have been estimated from isotonic twitches because of the difficulty of maintaining tetanic tension (504). Reported contraction times to peak force, which are inversely related to shortening velocity, vary by over 200-fold [mean = 0.010 s \pm 0.183 S.D.; range 0.004–0.79 s; (118, 287, 296, 416, 462, 479)].

Temperature

Temperature has a significant effect on the time course of muscle contraction in invertebrates (309). In locust and tettigoniid wing muscles, the rate of tension rise and decay in an isometric twitch increases and the twitch duration decreases as temperature is increased.

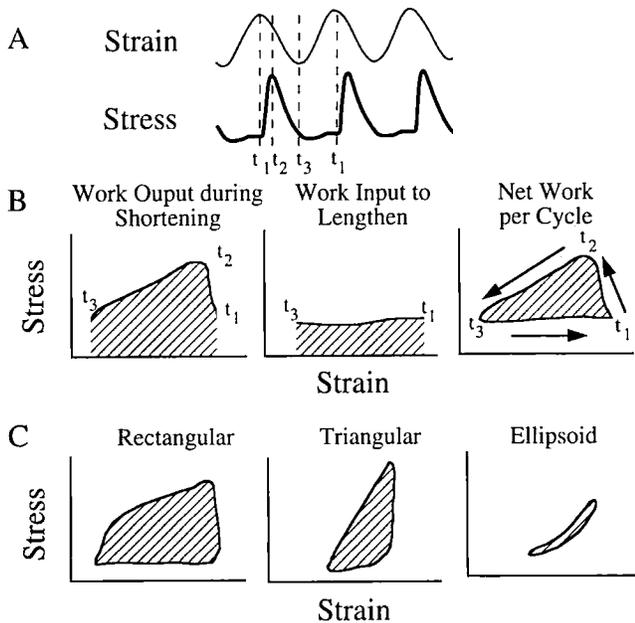


FIG. 12.9. Work-loop method to determine power output of an isolated muscle. *A*: Muscle is subjected to cyclic length changes (strain) while force per area (stress) is measured. The stimulation pattern is controlled. *B*: Area under the stress-strain curve represents energy produced (output) during shortening or absorbed (input) during lengthening. The difference between the curves represents the net work per cycle. Counterclockwise loops result in energy production, whereas clockwise loops result in energy absorption by the muscle. *C*: Variation in work-loop shape. Rectangular shape observed at low frequencies (<30 Hz). Triangular shape observed at intermediate frequencies (30–60 Hz). Ellipsoid shape observed at high frequencies (60–180 Hz) (after ref. 311).

At high rates of movement, the time for tension development and decay may become critical for propulsor movement (360). If muscle contraction time is long relative to the cycle time of the propulsors, then overlapping activity may occur in antagonistic sets of muscles, thereby reducing the power output available for segment movement (309).

The extent to which isometric twitch tension changes with temperature is more complex (309). Isometric twitch tension can be increased by an increase in shortening velocity at a given load or by an increase in twitch duration. Both can allow more stretching of the series elastic elements (apodemes). Increasing temperature in insect muscle increases the velocity of shortening but decreases the duration of twitch. The magnitude of twitch tension depends on which changes more. In locust flight muscle, isometric twitch tension increases by a factor of 2 with a temperature rise of 14°C (for example, 11°–25°C). At higher temperatures, isometric twitch tension is relatively independent of temperature.

Muscle–Organism Level

Sarcomere and muscle models (269, 270, 402, 480, 481) for determining or predicting force, velocity, and instantaneous power output of muscles move us closer to integrating muscle function to the level of whole-animal movement. If the role of individual muscles is to be understood, we must improve our estimates of musculoskeletal force (including fiber type differences), consider joint and segment geometry (mechanical advantage), include the frequency of movements (rhythmic oscillations) and the timing of muscle activation in a cycle, estimate energy flow into and out of segments to which muscles attach (energy transfer and storage of elastic strain energy), and link the segmental energy to the mechanical energy output of locomotion in the whole animal as discussed previously (Fig. 12.1). This has proven to be very challenging because muscles are numerous and variable and operate in three-dimensional space, but significant progress using invertebrates has been made.

The link between muscle function and whole-animal movement can be approached from “forward” or “inverse” directions using both experimentation and modeling (193, 481). Forward dynamics involves measuring or estimating musculoskeletal stress and strain to predict force, using force to determine joint moment, using joint moments and cycle frequency to calculate segmental energy, and using segmental energy to estimate mechanical power output (progressing from left to right in Fig. 12.1*B*). Inverse dynamics involves measuring or estimating mechanical power output, determining segmental energy, using segmental energy to calculate net joint moment, and using net joint moment to estimate musculoskeletal stress and strain (progressing from right to left in Fig. 12.1*B*). Both techniques have advantages and disadvantages and should be used in concert when possible. Research on insect flight serves as an excellent example of the desired interplay between the two approaches (172). I discuss the forward approach from sarcomeres to segmental energy, pointing out areas in which an inverse approach is more valuable.

Muscle Mechanical Power Output. Instantaneous power output calculated from the product of force and velocity derived from isotonic force–velocity curves allows comparison of different muscles. Instantaneous power output is maximal when the muscle’s shortening velocity is 0.2–0.4 v_{\max}^M . This “important range of speed” has typically been used (423) in conjunction with the simple optimality hypothesis proposed by Hill (270): “Each muscle is designed for maximal power and efficiency in its important range of speed.”

Unfortunately, isotonic contractions, isovelocity shortening, and slack test conditions do not mimic muscle function in most animals. Propulsive units most often function rhythmically. Instantaneous power output estimates do not consider frequency of movement nor do they mimic the neural stimulation pattern in animals. As a result, instantaneous muscle power output overestimates power output of a propulsor by two- to three-fold because the muscle in an animal is usually not generating power for half or more of the cycle. Estimates of sustained power output that include frequency have been attempted by assuming that the muscle is inactive for half the cycle (126). Other estimates assume that muscles shorten and lengthen at a constant or linear velocity (408, 508). Still other estimates assume a constant force during shortening, which instantaneously drops to zero during lengthening (407).

Muscle power output (P^M) can be written as a function of muscle force (F^M), change in muscle length (ΔL^M) and cycle frequency (ϕ):

$$P^M = F^M \Delta L^M \phi \quad (12-25)$$

or mass-specifically (per unit muscle mass):

$$P^{M*} = \sigma^M \epsilon^M \phi / \rho \quad (12-26)$$

where σ^M represents muscle stress (F^M / A^M), ϵ^M is strain ($\Delta L^M / L_0^M$), and ρ is muscle density.

Muscles rarely shorten at a constant velocity during locomotion but lengthen and shorten in a more sinusoidal fashion (304, 314, 315). Muscle force or stress varies with length, activation, velocity, and pennation angle. Imposing sinusoidal length and velocity changes on muscle reduces power output estimates by as much as 20% compared to estimates assuming linear or constant velocity shortening (314). Using the sinusoidal technique, muscle is subject to cyclic length changes and stimulated at a distinct phase in the motion while muscle force and length are recorded [(311, 349); Fig. 12.9]. From muscle stress and strain, a work loop is formed. Net work equals the work done during shortening minus the work done during lengthening; if the shortening, or positive, work exceeds the lengthening, or negative, work, energy is generated by the muscle (there is a positive, counterclockwise loop for stress vs. strain); if the positive work is less than the negative work, energy is absorbed by the muscle (there is a negative, clockwise loop).

One major advantage of the sinusoidal shortening approach is that the stimulation pattern used by the animal can be better approximated. In addition, stimulus phase, interstimulus interval, and the number of stimuli per cycle can be optimized at each cycle fre-

quency to determine maximum power output. Stimulation values and patterns used by an animal during locomotion can be determined from EMG recordings and compared to those giving maximum power output.

By measuring the power output of scallop adductor muscle under conditions representing those in vivo (362), Marsh and Olson (361) showed that the time course of power output for sinusoidal length changes still differed from the rate during natural length changes. Instantaneous force-velocity estimates from natural length trajectories revealed that scallop muscle did not operate on its isotonic force-velocity curve 60%–70% of the time. Obviously, the steady-state force-velocity curve sets an approximate range on function (452). Actual force-velocity trajectories are certainly complex and subject to transient variation of muscle activation (354), shortening deactivation, and stretch effects (238, 315, 317, 361). Precise knowledge of muscle length trajectories is essential for muscle power output estimates. Direct measures of muscle length change (222, 362) and accurate appendage kinematics during the locomotor cycle should receive more attention in the future.

Body Mass

Two different predictions follow from the proposed hypotheses concerning the relationship between body size and muscle power output.

One prediction, from Pennycuick and Rezende (408), states that muscle stresses are similar in animals that differ in size; therefore, animals activate some constant fraction of muscle area relative to the maximum. Strain is also mass-independent, which allows operation on the same region of the force-length curve. Mass-specific work per cycle would be independent of body mass. Muscle mass-specific power must be, therefore, proportional to cycle frequency. Since muscles are nearly a constant percentage of body mass, body mass-specific power would be proportional to frequency: if frequency scales to $m^{-1/3}$, where m is mass, then mass-specific muscle power should scale to $m^{-1/3}$. Small animals could have relatively more power available than large animals.

One point of contention with the Pennycuick and Rezende (408) model is that constant strain for all species means that intrinsic muscle shortening speed must scale with frequency, assuming muscles operate on a similar portion of the force-velocity curve. Small invertebrates, however, may reach limits on intrinsic speed such that strain must decrease when operating at high frequencies. Josephson (315) has shown that the constant strain model (using a constant 15% strain) applied to locust flight muscle operating at 20 Hz

results in the impossible conclusion that the muscle must contract at speeds greater than $u_{\max}^M (> 6 L_o^M/s)$ when attaining maximal power output.

Data, primarily from work on insect flight muscle using sinusoidal shortening, point to a second prediction distinctly different from the Pennycuick and Rezzende model (172; R. D. Stevenson and T. M. Casey, unpublished analysis). Maximal mass-specific muscle mechanical power output appears to change little with body mass and frequency (Fig. 12.8A), as shown by the observation that cycle frequency decreases with an increase in mass but mass-specific work per cycle increases. Mass-specific muscle work per cycle decreases with an increase in frequency due to a decrease in stress (fivefold for a 100-fold change in frequency) (Fig. 12.8B), a decrease in strain (sixfold) and a change in the shape of the work loop (R. D. Stevenson and T. M. Casey, unpublished analysis). Work loop shapes tend to show the following patterns (Fig. 12.9):

1. Rectangular for larger body mass and lower frequencies (<30 Hz). Higher force can be due to multiple stimuli.
2. Triangular at intermediate masses and frequencies (30–60 Hz). Forces result from twitches generated by one or two stimuli per cycle.
3. Ellipsoid at small masses and high frequencies (60–180 Hz). Asynchronous flight muscles fall into this category and never reduce minimum stress to zero.

Support for the hypothesis that mass-specific muscle power output does not scale to $m^{-1/3}$ also comes from an inverse dynamics approach. Mass-specific whole-body mechanical power output appears to be relatively independent of body mass (Fig. 12.5). For fliers in particular, Ellington (172) has argued that mass-specific induced power of the whole animal during flight scales with $m^{0.13}$ and work per cycle to $m^{0.46}$, based on studies of fliers taking off with loads attached (359). Total mass-specific power output should scale as induced power, as long as profile power (25%–30% of the total power output) and the reduction of inertial power by elastic strain energy storage scale to a similar power of body mass (172). If total mass-specific power output is representative of muscle, then muscle mass-specific power output might scale with a positive exponent or be more nearly independent of body mass.

If these predictions from the limited data on work loops are representative of invertebrates in general, then muscles of large or slow invertebrates operating at low frequencies would be predicted to show higher strain, lower strain rates, higher stress, longer relaxation time, and more mass-specific work per cycle. Muscles of small or fast invertebrates operating at

higher frequencies would be predicted to show lower strain, higher strain rate, lower stress, shorter relaxation times, and less mass-specific work per cycle.

Temperature

Maximum muscle power output has been shown to increase with temperature at a Q_{10} of 2 in the indirect flight muscle of moths (453). Mean power output increases from 20 to 90 W/kg muscle when temperature is increased from 20° to 40°C. The cycle frequency that produces maximum power output increases with temperature from 13 to 28 Hz. Work per cycle at the optimum frequency optimum strain both increase over this temperature range. The power output necessary for flight is approximately 50 W/kg muscle, based on estimates of whole-animal mechanical power output in hovering flight (171). Muscle mechanical power outputs of this magnitude are not observed until muscle temperature is greater than 30°C. Therefore, these findings are consistent with the observation that sphinx moths cannot take off at body temperatures less than 30°–35°C (254).

Fiber Types

Insufficient data are available to allow a comparison of invertebrate locomotor muscles that differ in fiber type. Fast fibers in fish produce more mass-specific power and at a higher cycle frequency than slow fibers (304, 423). Slow fibers can produce very little power at high cycle frequencies, where fast muscles operate, but show greater endurance.

Comparisons of maximal power output in different fiber types require that the volume of myofibrils be considered. Slow muscles with greater endurance have more mitochondria occupying muscle volume and would be expected to have lower mass-specific power outputs. Fast, anaerobic fibers give greater mass-specific power outputs partly because mitochondria occupy a smaller portion of the fiber, but these fibers fatigue more rapidly than slow fibers. Fast muscles do have a higher volume percentage of sarcoplasmic reticulum, which decreases mass-specific power output. Fibrillar or asynchronous insect flight muscle has relatively little sarcoplasmic reticulum but is still rapid because it functions by stretch activation and not direct neural signals (308).

Mechanical Advantage and Moments. The force and velocity with which a segment or appendage is moved cannot be predicted from muscle dynamics alone. Small muscle forces (F^M) can be made large at the end of the segment or skeletal element (F^S) to which the muscle is attached, and slow muscles can move segments rap-

idly. The transmission of force and velocity to a segment depends on mechanical advantage (F^S / F^M) or the velocity ratio (r / R , where r represents the muscle's lever arm and R the perpendicular distance from the point of force development by a segment to the axis of rotation) (11). To maximize force at an appendage or segment in a second-order lever where

$$F^S = (F^M r) / R \quad (12-27)$$

F^M and r are maximized and R minimized. To amplify or maximize the velocity of a segment (u^S) to which a muscle is attached

$$u^S \sim (u^M R) / r \quad (12-28)$$

u^M (muscle velocity) and R are maximized and r minimized. Obviously, maximizing force and velocity in the same lever system is not possible. Still, even these relationships do not allow one to predict the design of a musculoskeletal arrangement because of the possibility of equivalence (219). If the moment about a joint (M^J) is equal to

$$M^J = F^M r \quad (12-29)$$

or

$$M^J = \sigma^M (V^M / L^M) r \quad (12-30)$$

and the angle (ϕ^J) through which the joint rotates is approximately

$$\phi^J = \epsilon^M L^M / r \quad (12-31)$$

where ϵ^M is muscle strain, then neither the moment nor the angle is changed by altering fiber length, provided that the muscle's moment arm is changed so that the ratio L^M / r remains constant. A muscle with short fibers and a small moment arm can be equivalent to one with long fibers and a large moment arm (10).

Several muscles often span a joint (two connected segments in some invertebrates). Since the line of action of each muscle changes with time during locomotion; the moment arms must change with time. As a result, estimating an individual muscle's force over time even from reliable estimates of joint moments is often an indeterminant problem. The total moment is the net sum of the cross-product of all force vectors and moment arm vectors as a function of time (281). Analysis of mechanical advantage and muscle moments in invertebrate locomotion is a promising area for future contributions toward a link between neural control, muscle function, and segment movement. Data are currently sparse.

Full and Ahn (195) have developed a three-dimensional musculoskeletal computer model of a cockroach leg which demonstrates the importance of moment arms in interpreting muscle function (Fig.

12.10). Maximum moment arm varied by nearly two-fold among six femoral extensor muscles but was far more sensitive to joint angle. The model's predictions of joint moment were striking because moment arm length decreased to zero and switched to the opposite side of the center of rotation at joint angles within the normal range of motion. At large joint angles ($>100^\circ$), extensors acted as flexors to rotate the leg away from its maximum extension. Certainly, the effect of the muscle's action on leg function cannot be assessed without exoskeletal morphological data, even if isolated muscles are well characterized.

Species

Alexander (12) scaled estimates of the maximum force per unit body weight generated by animals as a function of body mass. Insects appeared to have relatively low values, possibly because of a low mechanical advantage resulting from their thin tubular legs. Mechanical advantage in a locust hindleg changes from 0.006 when the knee is flexed to 0.03 when it is partially extended (48). Muscle moment arms in cockroaches result in extensor muscles of the metathoracic leg developing a total force equivalent to over ten times the leg ground reaction force observed (195). Mechanical advantages found for slow, strong dung beetles range from 0.06 to 0.13 (182). Fast running tiger beetles have lower ratios of approximately 0.03.

Size

Muscle moment arms are short in insects but are also quite short in small mammals compared to large mammals. The moment arm or velocity ratio (r/R) of a mouse is only about one-tenth that of a horse (57, 58). Extrapolation of the scaling of mammalian moment arm ratio to the size of a cockroach yields a prediction of 0.05. At least for cockroaches, the moment arm ratio of 0.1 (195), albeit small, is actually larger than estimated for a mammal of its mass. Exoskeletons of insects may not necessarily constrain the muscle moment arm length.

Energy Transfer

Musculoskeletal Attachment

The magnitude and timing of muscle force transmission to an attachment site are dependent upon the connections of muscle to the skeleton. Muscle force or power production may not match musculoskeletal force or power output. Peak muscle force production and the time to peak force during a twitch will vary depending on the stiffness of the muscle's attachment. Attachments include both external and internal struc-

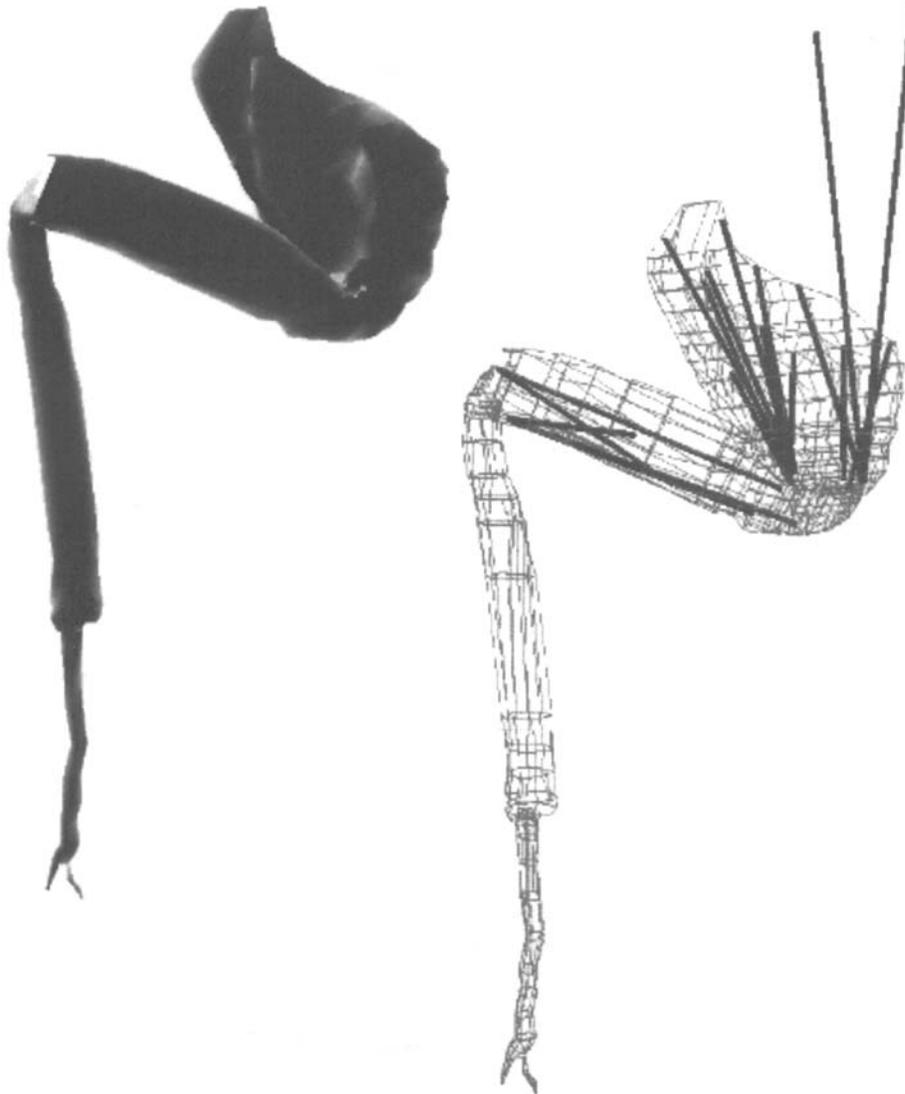


FIG. 12.10. Three-dimensional musculoskeletal model of the metathoracic leg of the cockroach *Blaberus discoidalis*. *Left*: Shaded polygons represent the exoskeleton, which was reconstructed from serial sections. *Right*: Heavy lines represent the lines of action of Hill-type muscles. The model is articulated at the coxa/trochanter–

femur and femur–tibia joints so that muscle lengths, moment arms, forces, and joint moments can be estimated for a range of body positions (195). The computer model was created using SIMM (MusculoGraphics, Evanston, IL).

tures, such as apodemes (the invertebrate tendon equivalent) that penetrate into pennate muscles. Stiff apodemes or connective tissue can transmit force rapidly, whereas a very compliant or slack apodeme may transmit less at particular joint angles. A relatively more compliant apodeme can result in greater fiber shortening, which may decrease force production (force–velocity dependence) and can delay peak force production if force builds later as velocity eventually slows (481). Including the whole musculoskeletal complex can alter the force–length curve. Maximum musculoskeletal force will be exerted by a muscle above resting length

because skeletal structures stretch and the angle of pennation decreases (529).

Full and Ahn (195) estimated the stiffness of the muscle–apodeme complex in cockroaches by calculating the ratio of apodeme slack length (length of apodeme beyond which it just begins to develop force) to optimal muscle fiber length [L_o^M (281, 529)]. Compliant muscle–tendon actuators have ratios greater than 1, which widen the ascending region of the force–length curve as well as increase the relative muscle length at which maximal force is attained. Values of the ratio range from 0.01 (gluteus maximus) to 11.3 (soleus)

in humans (281) and from 1 (semitendinosus) to 6 (plantarflexors) in cats (529). The ratio of the semitendinosus muscle of frogs is 1.5 (339). By comparison, cockroach extensor muscle–apodeme complexes appear relatively stiff (apodeme slack length to $L_o^M = 0.07–0.53$).

Energy Production and Absorption

Further influence of attachment tissues can be seen when a musculoskeletal complex undergoes cyclic length changes, as it does in many locomoting animals using rhythmic oscillation of propulsers. Depending on the timing of stimulation and the stiffness of the connective tissue or apodeme muscle may either generate and transfer energy to the segment through the apodeme or receive energy from the apodeme and absorb it (Fig. 12.1B). Muscles that generate power perform positive work, whereas negative work is done on muscles that absorb energy. If both of these functions are important to the musculoskeletal system, then in principle energy changes can be calculated from the net moments or torques (M^J) developed at each joint (the situation is obviously more complex for hydrostatic animals). The rate of work done by or to muscles varies with time. Instantaneous muscle power at a joint (P^M) (520) is the product of the net moment generated by the muscles at each joint and joint angular velocity ($\dot{\phi}^J$):

$$P^M = M^J \dot{\phi}^J \quad (12-32)$$

If the net muscle moments and joint angular velocity act in the same direction (that is, are both of the same sign), then the muscles are producing energy. If the net muscle moments and joint angular velocity act in the opposite direction (that is, they differ in sign), then the muscles are absorbing energy. If the segments to which the muscles are attached have the same angular velocity and are rotating in the same direction, then energy is transferred from one segment to another by muscles contracting isometrically.

If data on energy generation and absorption at joints are combined with energy transfer analysis, an even more complete picture of energy flow can be drawn. Energy transfer, generation, and absorption at a joint can be calculated from joint reaction forces and moments on segments (520). Energy transfer analysis of this type has not been attempted in invertebrate locomotion. The study of all forms of locomotion could benefit greatly from energy transfer analysis (70). This appears to be especially true in terrestrial locomotion, where positive work nearly equals negative work.

Full et al. (204) have combined three-dimensional kinematic data of running cockroaches with ground reaction force data (197) to calculate the net joint

moment and the net joint power for each major joint of all three leg pairs. Individual muscle groups were found to absorb as well as produce energy during the stance phase of running. Energy production and absorption differ among joints and legs. Femoral extensors produce most of the power during running, whereas coxal extensors mostly absorb energy. Hind- and middle leg muscles produce most of the power during running, whereas the front leg muscles primarily absorb energy. Estimates of muscle power from joint power are comparable to determinations derived from isolated muscle undergoing cyclic oscillations (194) and provide a link between leg dynamics and muscle function.

In insect flight and stridulation, Josephson (309) argued that energy produced by one muscle can be absorbed by its antagonistic pair. This results because the duration of the contraction exceeds the depression phase of the wing. This is most likely the rule rather than the exception, especially if muscle function involves stabilization, damping, co-contraction, and spring-like operation. Due to developmental and phylogenetic constraints, as well as multitask function, muscles are more likely to generate movement with only a component of their maximal force in the direction of movement during a particular task, even though this results in transfer to, and absorption by, other muscles and skeletal parts not contributing directly to propulsion.

Elastic Strain Energy Storage

Since energy transfer can be substantial, elastic strain energy storage systems are of potential importance (14). The amount of energy that can be stored ranges from 2 to 9 kJ/kg for tendon, apodeme, and rubbery materials (18, 49). If apodemes, ligaments, connective tissue, and skeletal elements obey Hooke's law, then the strain energy stored would be $F^S \Delta L^S / 2$, where F^S is the force causing deformation of the segment or skeletal component and ΔL^S the extension (11). Force can be written as $F^S = A^S \sigma^S$, where A^S is the cross-sectional area. Since strain ($\Delta L^S / L_o^S$, where L_o^S is the initial length of the structure) is equal to σ^S / Y , Y representing Young's modulus, then $\Delta L^S = L_o^S \sigma^S / Y$. Elastic strain energy is, therefore:

$$E^S = A^S \sigma^S L_o^S / (2Y) \quad (12-33)$$

Since materials do not obey Hooke's law, all energy is not recovered (rebound resilience < 1). Energy is lost as heat in the process of stretching and recoil (energy dissipation > 0).

In fibrillar flight muscle, the muscle itself may serve as a spring (14, 349). Flight muscles operating at high frequencies undergo small strains (< 3%) and do little

work per contraction. As a result, the muscle capacity for storing energy may make a significant contribution in these small fliers. If the storage capacity is as large as 1.3 J/kg muscle, then all of the kinetic energy involved in the deceleration of the bumblebee wing stroke could be stored in the muscle (157).

Bennet-Clark (48) has determined the material properties and energy storage of the extensor apodeme in jumping locusts. Jumping locusts store energy in their apodemes and the cuticle of the knee extensor muscles (48, 213). The specific energy storage of the locust extensor apodeme is three times that of resilin and about five times that of steel (51).

Muscles and their attachments (high stiffness, low strain) are not the only structures involved in energy storage and transmission. A variety of rubbery materials (for instance, resilin, abductin, and elastin) which function as elastomeric springs (low stiffness, high strain) may even replace a muscle and act as the sole muscle antagonist (224).

Locusts have pieces of a rubbery material called resilin at the base of their wing hinges (11, 14, 300, 505). Kinetic energy from the wings can be stored temporarily in the resilin as elastic potential energy when the wings are raised and then returned to the wings as they are lowered. Jensen and Weis-Fogh (300) found a high degree of energy return in locust resilin, comparable to rubber and some plastics (11). Dragonflies have resilin, but it is located in series with the apodemes to which only minor wing muscles attach (14, 506).

The click mechanism used in the flight of dipteran insects to drive the wings can involve energy storage (18). Elastic strain energy stored in the cuticle at the extremes in wing stroke position can be returned as rapid angular acceleration and rotation of the wing (177).

Dickinson and Lighton (148) have argued that the useful elastic strain energy storage in fruit flies is only 11%. Greater energy storage would not further reduce the power requirements of flight because the energy recovered by elastic storage is exactly offset by a loss in aerodynamic power savings (see 2 Comparison of Locomotor Dynamics, below).

Muscles in jumping locusts and fleas simply could not contract fast enough to produce the impulse generation necessary for their jumps. Fleas use resilin at the base of their hindleg (53). The resilin is compressed as the legs are raised slowly. The energy stored is released rapidly, propelling the leg downward.

Swimming scallops take advantage of an elastic protein found in the hinge of their shells, called abductin (323, 471). An adductor muscle closes the shell, but no muscle antagonist is present. The compression of

abductin upon shell closure results in energy storage, which is returned to open the shell. Young's modulus ranges from 1 to 4 MPa and rebound resilience is 0.91 (8).

Squid eject water by contracting circular muscles, which results in increasing the mantle wall thickness (225, 226). Elastic collagen fibers in the mantle wall are stretched by increasing its thickness. Stored strain energy can be released at a time in the jet cycle when the muscles are not generating their full mechanical power output. Because the stress-strain function is nonlinear, the elastic structures in the mantle are deformed easily early in the contraction, when hydrodynamic work is high, but increase stiffness at the end of the contraction to allow energy storage when hydrodynamic work is reduced. The potential energy in the elastic structures can be used to power refilling at slow speeds (227). During escape, refilling is aided by radial muscles.

Jellyfish show similarities to squid with respect to storage of elastic strain energy. Jellyfish decrease the diameter of their bell by contracting swimming muscles. This action increases the thickness of the body wall and stretches the radial mesoglea fibers (139). Calculations show that most of the energy stored in the mesoglea during contractions is stored as elastic strain energy and saves as much as 37% of the energy that would otherwise be generated by muscle (141). Action potentials in the jellyfish *Polyorchis* are unusually long and similar to cardiac potentials (140). The longer duration may allow for sufficient time late in the contraction to store elastic strain energy.

ENERGETICS OF LOCOMOTION

Muscles convert chemical energy from metabolism into mechanical energy to generate the forces and power output necessary for locomotion (Fig. 12.1A). Utilization of metabolic energy has received considerable attention because it allows an evaluation of the efficiency of the musculoskeletal system for physiologists and provides important bridges to ecology, behavior, and biochemistry. Metabolic power input is expected to vary with speed, size, mode of locomotion, species differences, and body temperature, as does mechanical power output. Once again, the rich natural variation in invertebrate locomotor energetics allows opportunities to test general hypotheses of function, offers a chance to speculate on limits of function, and provides tractable systems that can be manipulated experimentally.

The energetics of locomotion is most conveniently partitioned by the source of the energy into those

processes that require oxygen and those that do not. I first discuss the metabolic power input derived from aerobic metabolism, which tends to correlate with sustainable behaviors of longer duration, and follow with a consideration of nonaerobic metabolism (that is, high-energy phosphates and accelerated glycolysis) associated with shorter-term, high-intensity locomotion. I conclude with a comparison of the energetic cost of transport, the metabolic energy used to move a unit body mass a unit distance.

Aerobic Metabolism

Speed

Flying

The only study on free forward flight in insects shows that the rate of oxygen consumption is independent of speed (173). Bumblebees do not show a U-shaped curve for mechanical or metabolic power, as predicted from aerodynamic arguments. Rates of oxygen consumption for forward flight are comparable to those of hovering flight and are most likely not maximal since a variety of species can fly with heavy loads (359).

Running

In insects, myriapods, and crustaceans that reach a steady state, oxygen consumption tends to increase linearly with speed until a maximum is attained. Well-defined maximum rates of oxygen consumption have been observed in walking crabs (190, 199) and running cockroaches (210). In a desert beetle, *Onymaoris plana*, oxygen consumption plateaus at high speeds, which may signal a gait change since these speeds may be sustainable and oxygen uptake may not be maximal (44). In most species, the oxygen consumption vs. speed function does not extrapolate to resting or standard metabolic rate; rather, there is an elevated y intercept. Several reasons have been hypothesized for the increased cost at low speeds, including stress, lack of measurements at low speeds (that is, not detecting a curvilinear relationship), extraneous movement at low speeds on treadmills (160, 346), and a postural cost (262). Providing evidence for a postural cost (430), Herreid and Full (260) discovered that hermit crabs carrying a characteristic shell of twice their body mass show a typical y intercept elevation but no intercept elevation when walking without their shell.

Swimming

Few studies on swimming in invertebrates have measured oxygen consumption over a range of speeds, but those that have show similar patterns. In shrimp, oxygen consumption increases exponentially with

speed to the 2.6 power (293). Small paddling blue crabs increase oxygen consumption curvilinearly with speed (276). Oxygen uptake rates follow a similar function in squid and *Nautilus*, which correlate well with the jet pressure–speed function (399). By contrast, crabs and lobsters walking under water tend to increase oxygen uptake in direct proportion to speed (276, 278, 280). The underwater walkers tested thus far may not attain speeds where drag dominates metabolic cost. However, the water flow regime must be better characterized for bottom movers.

Crawling

Oxygen consumption of crawling snails (277, 292), slugs (143), and insect larvae (54, 97) increases linearly with speed over the narrow range of locomotor speeds. The same relationship is found for crawling on land and under water.

Size

Flying

Mass-specific oxygen consumption in hovering flight decreases by 3.5-fold over a three orders of magnitude increase in body mass (Table 12.3; Fig. 12.11). The mass-specific metabolic cost of flying in sphinx moths scales with mass to the -0.23 power, saturnids to the -0.41 power (39), and Euglossine bees to the -0.36 power (102). Oxygen consumption may scale proportionally with body mass in some lepidopterans because the smallest fliers have a relatively low cost due to low wingbeat frequencies and an inability to regulate their thoracic temperature during flight (96). Robber flies show a proportional increase in metabolic cost with body mass (384). Mass-specific rates are significantly lower than other asynchronous fliers, such as the hymenoptera.

Running

Mass-specific oxygen consumption rates measured in walkers and runners decrease by nearly 50-fold with an increase of six orders of magnitude body mass (Table 12.3; Fig. 12.11). This relationship represents adjusted oxygen consumption rates for body temperature differences, assuming a Q_{10} of 2 since rates increase with temperature. The reason for the elevated oxygen consumption rates is that beetles, cockroaches, and perhaps other runners warm up during walking (38, 209; Fig. 12.11 open circles with dots in center). The relationship for insect runners that do not warm up changes less with body mass (Fig. 12.11B). Mass-specific consumption rates of crustaceans decrease the slope of the general scaling relationship because of their relatively low values (that is, these invertebrates

TABLE 12.3. *Scaling of Oxygen Consumption as a Function of Body Mass*

Mode	Name (Taxonomic Group)	Oxygen Consumption ($\text{ml O}_2 \cdot \text{kg}^{-1} \cdot \text{s}^{-1}$) = $a m^b$			r	n	P
		Mass Range (kg)	b (S.E.)	log a (S.E.)			
Runners	All	0.000001–0.225	–0.324 (0.051)	–1.272 (0.154)	0.61	70	<0.001
	Insects	0.0000047–0.0054	–0.123 (0.058)	–0.516 (0.187)	0.30	50	0.038
	Crustaceans	0.0021–0.225	–0.316 (0.114)	–1.398 (0.215)	0.70	10	0.024
Swimmers	All	0.00001–0.905	–0.152 (0.077)	–1.534 (0.224)	0.47	16	0.068
Fliers	All	0.0000016–0.0028	–0.161 (0.049)	0.674 (0.169)	0.44	48	0.002
	Bees, flies, mosquitoes (Hymenoptera, Diptera)		–0.120 (0.041)	0.918 (0.155)	0.65	14	0.012
	Moths (Lepidoptera)		–0.124 (0.083)	0.843 (0.266)	0.29	26	0.148

are large and have a lower intercept than the smaller insects). Arachnids are distinct from other runners in having the lowest mass-specific oxygen consumption rates, but few measurements are available.

Swimming

Mass-specific oxygen consumption rates measured in swimmers and underwater walkers decrease by nearly 6.6-fold with an increase of five orders of magnitude body mass (Table 12.3; Fig. 12.11).

Jet Propulsion and Crawling

Insufficient data are available to scale oxygen consumption with mass in jetters and crawlers. A far greater size range needs to be studied in crawlers.

Mode of Locomotion. Aerobic power input during activity in invertebrates varies by over 10,000-fold, from 0.003 to 40 $\text{ml O}_2 \cdot \text{kg}^{-1} \cdot \text{s}^{-1}$ (Fig. 12.11). The aerobic capacity of 1 g fliers is 28 times that of an average 1 g runner. The aerobic factorial scope (ratio of active to resting oxygen consumption) is 129-fold in flying insects (Fig. 12.12). These extraordinary aerobic rates translate into a mitochondrial oxygen consumption that ranges from 6–16 $\text{ml O}_2 \cdot \text{ml mitochondria}^{-1} \cdot \text{min}^{-1}$ compared to values of 1–6 $\text{ml O}_2 \cdot \text{ml mitochondria}^{-1} \cdot \text{min}^{-1}$ for aerobic vertebrates (99).

Runners that warm their bodies during locomotion approach the rates of fliers and have factorial scopes of 26-fold. A 1 g runner consumes six times more oxygen than a swimmer of the same mass. The most aerobic invertebrate swimmers approach the aerobic

rates of runners. The aerobic capacity of 1 g swimmers is over five times that of crawlers and jellyfish jet propulsors (Fig. 12.11, lighter shading). Squid jet propulsors have the highest aerobic capacity among aquatic animals relative to their mass (Fig. 12.11, dark shading).

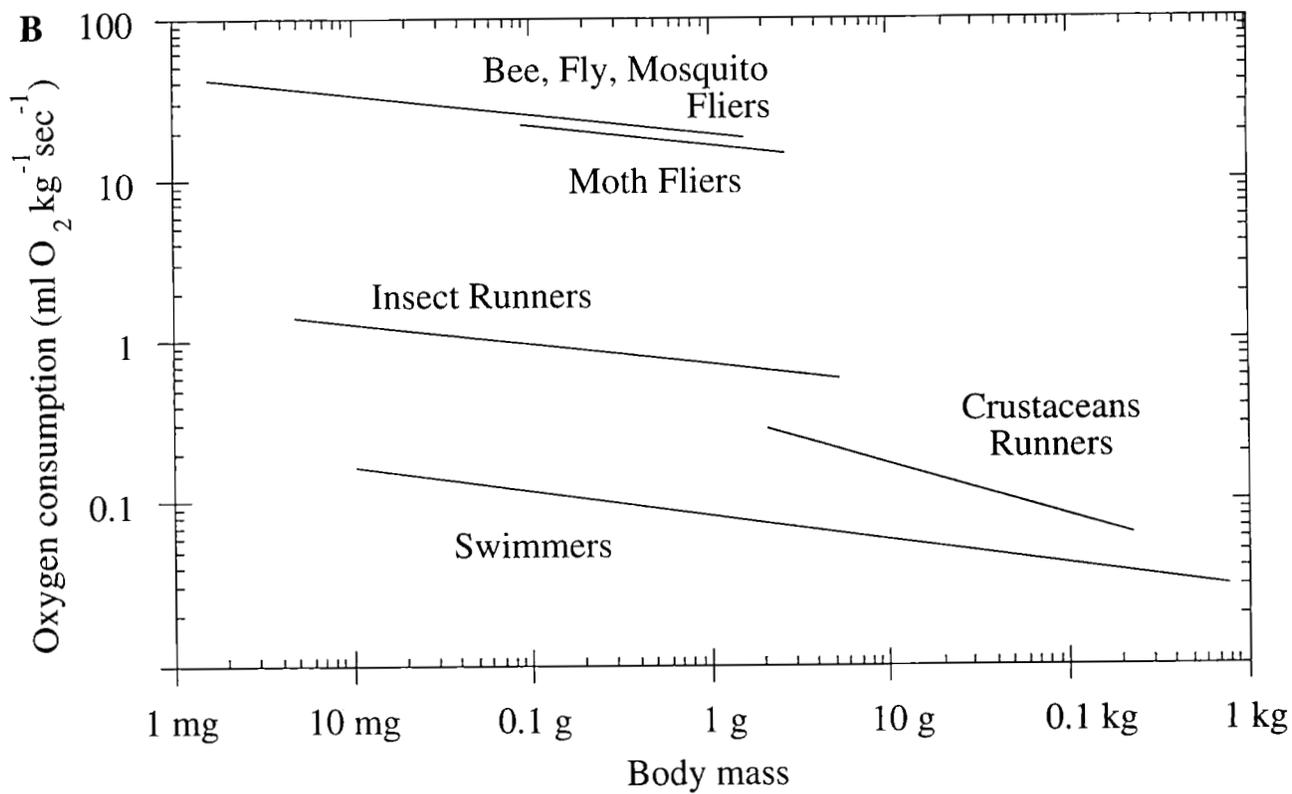
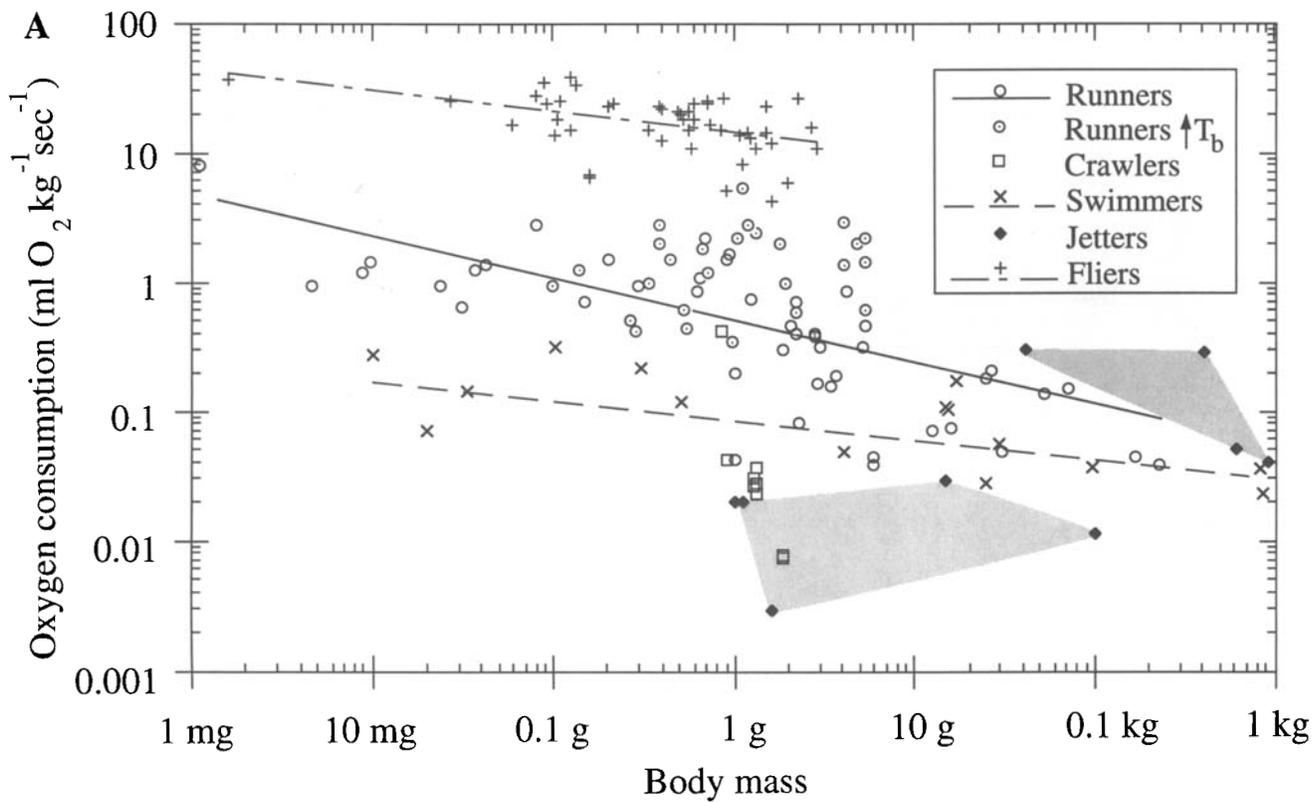
Species

Flying

Variation in oxygen consumption during flight in insects is associated with wing morphology and operation (96). Euglossine bees have among the highest mass-specific rates of oxygen consumption measured in fliers that range in mass from 0.1 to 1 g. These relatively high rates correlate with the euglossine bee's small wings and high wingbeat frequencies. Bumblebees have higher wing loading (that is, weight supported/wing area) than honeybees and exhibit higher rates of oxygen uptake. Sphinx moths have higher metabolic rates than saturnid moths of the same body mass, most likely because of their relatively small, narrow wings (39). Casey (96) points out, however, that oxygen consumption, flight performance, and thoracic temperature do not correlate well with wing loading alone.

Running

Running and walking insects consume oxygen at higher rates than other terrestrial locomotors even when the effects of size are removed. The high rates are in part due to the increased thoracic temperature in



walking beetles (38) and cockroaches (209). However, aerobic factorial scopes of insects that do not generate a large amount of heat (Fig. 12.12) still exceed, on average, those measured in myriapods, crustaceans, and arachnids. A 1 g insect that does not warm can have oxygen consumption rates during running that are twice that of a crustacean and five times that of an arachnid of the same mass.

Swimming and Jet Propulsion

In general, aerobic factorial scopes are lower in swimmers than runners. Cephalopod molluscs are the most aerobic, approaching rates observed in runners (398). Jellyfish (338) and swimming salps (351, 474) are the least aerobic for their mass, having aerobic factorial scopes of less than 2. Locomotor muscle in both groups represents 1% or less of body mass.

Crawling

Aerobic factorial scopes are very low in crawlers. Gastropods can increase oxygen consumption by only about twofold or less over resting rates (277, 292).

Temperature and Dehydration

Flying

Oxygen consumption in flying insects, including sphinx moths, lasiocampid moths, lymantriid moths, bumblebees, and honeybees, is independent of air temperature (96). In many species, a minimum thoracic temperature is necessary for takeoff and flight. Large species in particular actively regulate thoracic temperature over a wide range of environmental temperatures (255). Honeybee workers can fly at 45°C and not overheat because they regurgitate fluid from their stomachs onto their heads for evaporative cooling (252, 253).

Running

The highest rates of oxygen consumption during running are attained by beetles (38) and cockroaches (209) that warm the thorax in preparation for flight or when alarmed. Studies within a species show that the lowest active rates of oxygen consumption are attained at lower temperatures. Cockroaches and crabs exercising on treadmills increase oxygen consumption with temperature at most speeds (263, 500). Maximal rates of consumption increase with temperature in large tropical cockroaches and ghost crabs but decline at the highest temperatures (209, 500). Both the extent and the rate of dehydration can decrease the maximal rate of oxygen consumption in ghost crabs (501).

Swimming

Swimming blue crabs maintain an aerobic factorial scope of 4.6 at temperatures ranging 13°–28°C (75).

Anaerobic Metabolism

The high mechanical power outputs necessary to execute the most intense behaviors for brief durations are often derived from nonaerobic sources. Total energy output can be raised by 20-fold over resting rates in molluscs and by nearly 60-fold in crustaceans (536). Unfortunately, comparisons of nonaerobic metabolism across species, as has been done in the study of aerobic contributions, are problematic because work output is seldom quantified nor activity standardized.

One major misconception about nonaerobic metabolism during activity in invertebrates concerns the diversity of pathways given the seeming plethora of end-products used in environmental hypoxia and anoxia. High power output, nonaerobic metabolism used during locomotion (termed exercise or functional anaero-

FIG. 12.11. Whole-animal mass-specific metabolic power input as a function of body mass. Oxygen consumption rates are the highest available for the species. In some cases, they are known to be maximal rates. *A*: Oxygen consumption as a function of body mass for runners, crawlers, swimmers, jetters, and fliers. Shaded areas represent jetters; top right area includes molluscs such as squid; bottom area includes jellyfish. Insect runners can warm their bodies. The regression line shown is for the Q_{10} corrected data set not shown ($Q_{10} = 2$). Data include runners (22, 41–44, 190, 199–202, 210, 212, 258, 259, 261–266, 301, 343, 345–347, 368, 374, 427, 433, 514, 522; W. J. Van Aardt, unpublished data), runners with elevated body temperature (37, 209), crawlers (97, 277, 292), swimmers (119, 184, 276, 278, 279, 293, 328, 369, 371, 428, 466), jetters (29, 130, 338, 395, 399, 474, 495, 511), and fliers (36, 39, 42, 91–93, 96, 100, 102, 104, 108–110, 173, 250, 251, 273, 318, 333, 384, 393, 427, 447, 502, 507, 521). *B*: Oxygen consumption rates by taxonomic groups (Table 12.3). Data include insect runners (41–44, 210, 212, 259, 263, 266, 301, 343, 345–347, 368, 427); crustacean runners (190, 199, 200, 202, 261, 262, 264, 265, 514, 522; W. J. Van Aardt, unpublished data); swimmers (119, 184, 276, 278, 279, 293, 328, 369, 371, 428, 466, 474); moth fliers (39, 91–93, 96, 100); and bee, fly, and mosquito fliers (36, 42, 96, 102, 104, 108–110, 173, 250, 251, 273, 318, 333, 384, 393, 427, 447, 502, 507, 521).

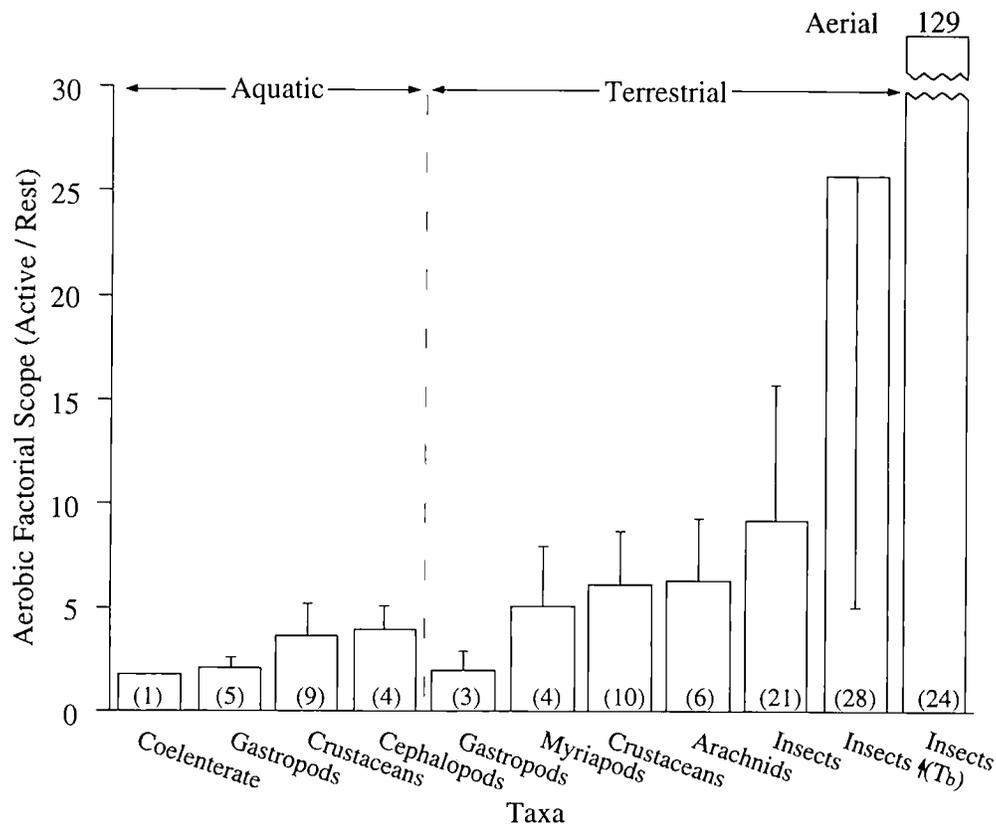


FIG. 12.12. Aerobic factorial scopes for invertebrate activity. Oxygen consumption rates are the highest available for the species. In some cases, they are known to be maximal rates. Bars represent ± 1 S.D. Numbers in parentheses are sample size. Data include aquatic groups such as coelenterates (338), gastropods (277, 292), crustaceans (119, 184, 276, 278, 279, 293, 328, 369, 371, 428, 466), and cephalopods (29, 395, 399, 495, 511); terrestrial groups such as gastropods (277, 292), myriapods (201), crustaceans (190, 199, 200, 202, 261, 262, 264, 265, 514, 522; W. J. Van Aardt, unpublished data), arachnids (22, 258, 347, 374, 433), and insects (41–44, 210, 212, 259, 263, 266, 301, 343, 345–347, 368, 427); insects with elevated body temperature (37, 209); and aerial groups such as insects (36, 39, 42, 91–93, 96, 100, 102, 104, 108–10, 173, 250, 251, 273, 318, 333, 384, 393, 427, 447, 502, 507, 521).

biosis) is largely distinct from the low-energy anaerobic metabolism employed during decreased environmental oxygen levels (536). All invertebrate phyla possess the lactate pathway (348). In some annelids and molluscs, pyruvate oxidoreductases coexist with or replace lactate dehydrogenase (LDH). These enzymes require pyruvate and an amino acid as cosubstrates. The compounds formed in conjunction with these enzymes are termed opines and include octopine, strombine, and alanopine. Opine formation is restricted to marine invertebrates. The pedal retractor muscle of cockles and whelks, the adductor muscle of swimming file shells and jetting scallops, and the mantle of squid produce one major end-product, octopine (536). The pedal retractor muscle of some gastropods forms octopine and strombine (28). The body wall muscle of the

marine worm *Arenicola* accumulates alanopine (438).

Crustaceans, insects, myriapods, and arachnids do not possess opine dehydrogenase activity and produce D- or L-lactate. Crustaceans (216, 532), scallops (112, 537), and some annelids (438) can accumulate succinate, but the small increase in concentration is associated with negligible contributions to energy production.

Another common difficulty with studies focusing on nonaerobic energy sources is the lack of concomitant oxygen consumption measurements (30). The use of aerobic and nonaerobic metabolism is not mutually exclusive. Both often contribute during an activity. There appears to be a continuum of energetic response patterns, depending primarily on the rate and duration of activity (262).

Aerobic Response Pattern. Aerobic responses to sustained exercise have been measured in insects (259, 263, 266), ghost crabs (190, 199), hermit crabs (260), centipedes, and millipedes (201). Oxygen consumption increases rapidly to a steady rate (time to one-half steady rate is 30 s to 3 min). Flying (496, 502) and running (205) insects have not been shown to rely on nonaerobic metabolism at even the highest activity rates. Flying insects have among the lowest concentrations of the high-energy phosphate store arginine phosphate (47). Although ghost crabs show an aerobic response pattern at sustainable speeds, accelerated glycolysis can result in net L-lactate production early in exercise at speeds that elicit greater than 70%–90% of maximal oxygen consumption (190, 199, 211). As exercise continues, net L-lactate removal results and the estimated ATP production from accelerated glycolysis is minor.

Mixed Aerobic and Nonaerobic Response Pattern. Most invertebrates have the capacity to generate and utilize ATP from both aerobic and nonaerobic sources when conducting moderate to intense activity. Non-aerobic sources are utilized either early in locomotion before steady state is attained or when locomotion exceeds the capacity for maximal oxygen transport.

Crustaceans

Several semiterrestrial and terrestrial crabs (200, 264, 265, 523) show a sluggish aerobic response to locomotion (time to one-half steady rate is 4–6 min) and most likely rely on contributions from accelerated glycolysis (522). Fiddler crabs rely on accelerated glycolysis extensively before oxygen consumption increases (200). Aerobic ATP production increases modestly with speed, and accelerated glycolysis accounts for 40% and 70% of the energy at low and high speeds, respectively. Christmas Island red crabs attain maximal oxygen consumption within 5 min of walking and after 45 min show some of the highest lactate concentrations measured for crustaceans (2). During underwater walking, the shore crab *Carcinus* increases oxygen consumption rapidly at speeds below that which elicits maximal oxygen consumption but supplements energy production with accelerated glycolysis by 4%–42% (280). Swimming blue crabs show elevated muscle and hemolymph lactate levels during steady-state oxygen consumption yet do not fatigue easily (74, 76, 77). Perhaps branchial excretion of H⁺ to the ambient water and modulation of hemocyanin by lactate aids fatigue resistance (76, 77).

Arachnids

Tarantulas attain a steady rate of oxygen consumption rapidly but always appear to be exercising at

their maximal oxygen consumption even at the slowest speeds that they sustain (22). The production of D-lactate can account for as much as 30% of the ATP required for locomotion. In three species of spider studied during a 2 min struggle, the proportion of support by accelerated glycolysis ranged from 55% to 94% (412). The rate of D-lactate accumulation is inversely proportional to the surface area of the respiratory organ, the book lungs (411).

Molluscs

File shells employ predominantly aerobic metabolism to power 5 min of sustained swimming using shell closures (30). Accelerated glycolysis plays only a minor role, but 23% of the energy comes from the depletion of arginine phosphate.

Annelids

Nereis, which crawl on the bottom, have the capacity for D-lactate formation; however, when they become mature and swim by undulation, no lactate production is observed and swimming is powered by aerobic metabolism (432).

Nonaerobic Response Pattern. The highest intensity exercise in many invertebrates relies on the breakdown of stored high-energy phosphates and accelerated glycolysis. The duration of the activity, most often escape, is on the order of seconds. Greater reliance on stored high-energy phosphates (for example, arginine phosphate) and higher resting concentrations correlate with the greatest power outputs (536). Larger contributions of glycolysis are associated with lower rates of ATP utilization compared to the stored high-energy phosphates.

Arachnids

Some of the best evidence for these hypotheses comes from studies on running spiders (413, 414). The quantified, rapid decline in speed after 10–20 s of escape is likely to be the result of the complete depletion of arginine phosphate in muscle and not the buildup of anaerobic end-products or the lack of circulation to the legs. Rates of D-lactate accumulation increase only after 10 s. The highest rates of D-lactate formation are not associated with the highest running speeds.

Crustaceans

The initial burst of tail flipping in a yabby (crustacean) is powered by arginine phosphate, and only later, during a series of less powerful tail flips and a defensive posture, does L-lactate increase (176). Escaping shrimp using tail flips appear to show the same pattern (400). *In vivo* ³¹P nuclear magnetic resonance (NMR) has

revealed that prawns more tolerant to anaerobiosis are better able to maintain ATP levels as arginine phosphate decreases during bursts of muscular exercise (464). Ghost crabs require nonaerobic metabolism during trotting, when fatigue occurs 36–50 s after traveling 20 m (206). Both accelerated glycolysis and high-energy phosphates contribute significantly to energy production. Muscle L-lactate content increases eightfold and arginine phosphate levels decrease nearly fivefold below preexercise levels. The wharf crab *Sesarma* has the lowest aerobic capacity of any crustacean measured. It can increase oxygen consumption by only 60% over rest and has limited endurance, but the source of the energy requires further investigation (202).

Molluscs

Jet propulsion in scallops is powered by arginine phosphate (80%) and ATP depletion (20%) (236). No octopine or lactate is produced until after fatigue and during recovery. Squid show a similar pattern after 10 s of vigorous swimming to fatigue (456). Exhaustion in cuttlefish also results in the complete depletion of arginine phosphate and the formation of octopine (457). None of the other typical end-products found after anoxia has been found to increase in concentration after exercise.

Insects

Jumping in grasshoppers and locusts is powered by high-energy phosphate depletion (70%) and, at least in part, by accelerated glycolysis (30%), shown by an increase in L-lactate (272). Accelerated glycolysis accounts for only 7% of the total energy consumed during 5 min of escape hopping in two-striped grasshoppers, whereas aerobic metabolism supplies the remainder (246).

Recovery from anaerobic metabolism in invertebrates has been discussed in numerous publications (174, 200, 256, 442).

Endurance and Metabolism

Metabolic response patterns correlate well with endurance in invertebrates. The most aerobic fliers have remarkable endurance, given the rates of expenditure. High power output escape by arachnids (414), crustaceans (206), and molluscs, which relies on high-energy phosphates, typically lasts only seconds. Endurance of invertebrates using mixed aerobic and nonaerobic responses ranges from seconds to as long as 15 min (257). Studies on invertebrate runners provide the most apparent link between energy metabolism and endurance because speed or work output, maximal oxygen

consumption, and in several cases anaerobic end-products have been quantified.

Continuous Locomotion. The capacity to sustain continuous locomotion is a function of, at least, speed, aerobic capacity, metabolic cost, temperature, and dehydration. In general, the lowest speeds or activity levels are supported by aerobic metabolism. As speed increases, eventually a work load is reached that can no longer be supported by aerobic metabolism alone. Oxygen consumption attains a maximum when an increase in speed does not elicit a further increase in oxygen uptake. The speed at which oxygen consumption becomes maximal and nonaerobic sources support subsequent increases in speed is referred to as the maximal aerobic speed (302). The correlation between endurance and the maximum aerobic speed is high. As crustaceans (190, 199, 200, 202, 280, 500, 501, 523) and insects (209) approach their maximum aerobic speed, endurance decreases from hours to just 2–15 min.

Size

Large invertebrates have high rates of aerobic metabolism relative to smaller species and, therefore, would be predicted to have greater maximal aerobic speeds. However, mass-specific oxygen consumption scales with body mass such that smaller animals have relatively higher rates. This tends to decrease the differences in maximum aerobic speed in large and small animals. Maximal oxygen consumption scales with the 0.70 power in ghost crabs that range in mass from 2 to 71 g (190). As predicted, 27 g individuals have a higher maximum aerobic speed than 2 g animals and a concomitantly greater endurance capacity. However, the largest crabs have poorer endurance and a lower maximum aerobic speed than do 27 g animals. The maximal rate of oxygen consumption alone is an insufficient predictor of sustainable activity, despite many claims to the contrary. It is the interaction of the metabolic cost of locomotion and maximal oxygen consumption that determines the maximum aerobic speed and endurance (189, 196, 211, 220).

Metabolic Cost of Locomotion

Two invertebrates with the same maximal aerobic capacity do not necessarily have the same endurance. If activity costs more for one than the other, the less economical animal will attain its maximum aerobic speed at lower speeds and will fatigue at lower power outputs. Small animals have a higher mass-specific oxygen consumption than large animals (Fig. 12.11) but a higher mass-specific cost of transport (Fig. 12.13). Small animals tend to have lower maximal aerobic speeds than larger animals and fatigue at slower speeds.

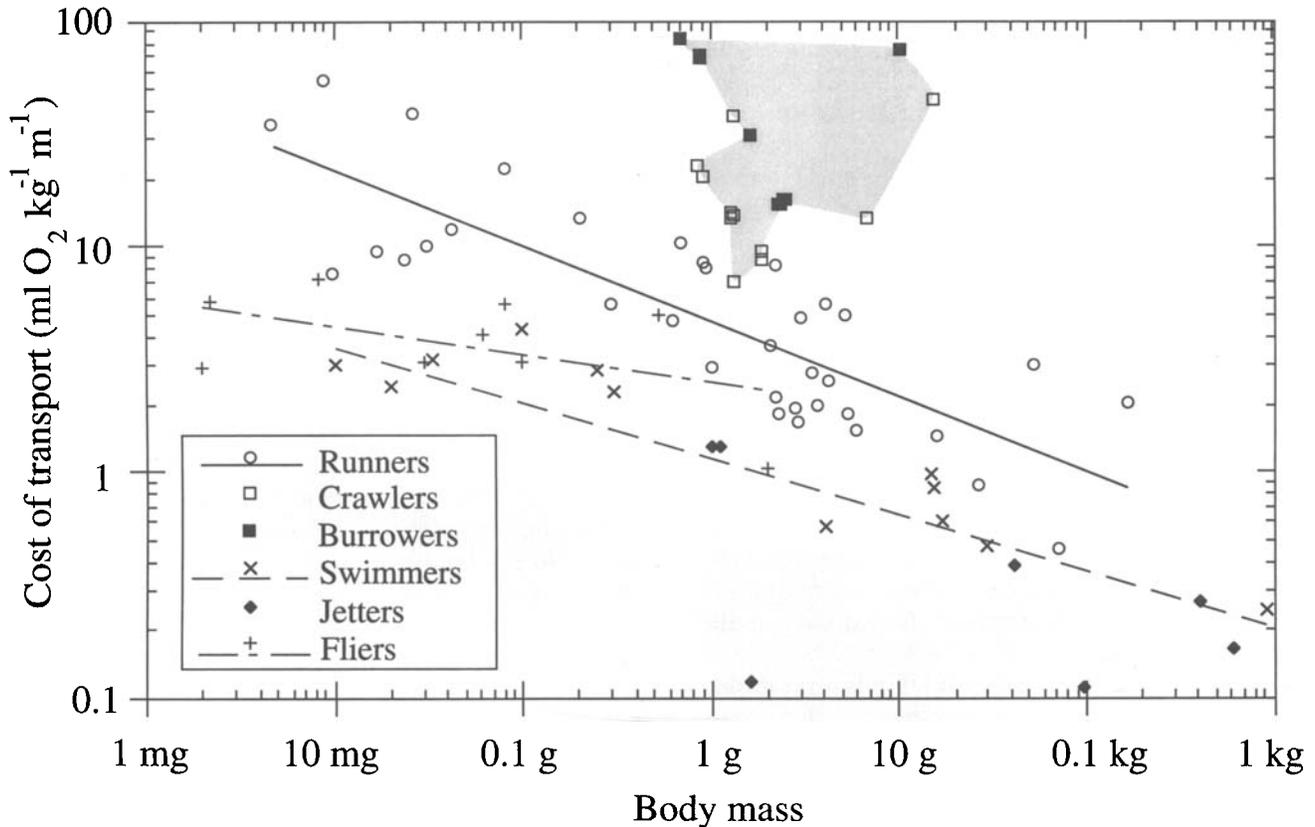


FIG. 12.13. Mass-specific metabolic cost of transport as a function of body mass. Values represent minimum cost of locomotion available. Shaded area represents hydrostatic crawlers and burrowers. Data include runners (41, 43, 44, 55, 159, 191, 199–201, 209, 212,

259, 260, 263–265, 301, 343, 345–347), crawlers (97, 143, 267, 277, 292), burrowers (54, 291, 469), swimmers (119, 184, 241, 276, 278, 280, 293, 328, 369, 468, 474, 511), jettors (130, 338, 395, 399, 495), and fliers (173, 273, 478, 483, 503, 521).

Variations can occur within a species. For example, large ghost crabs (71 g) fatigue at maximal aerobic speeds that are slower than those of 27 g animals because the sideways walking in large crabs is relatively costly (190).

Temperature

Temperature affects the maximal rate of oxygen consumption and, therefore, maximum aerobic speed and endurance. Maximal rates of oxygen consumption typically increase with temperature by Q_{10} values of near 2 until a maximum is attained. At the highest temperatures, maximum oxygen consumption remains the same or decreases. Maximal aerobic speed and endurance reflect these changes in walking crabs (211, 500) and cockroaches (209). From low to preferred temperatures, maximum oxygen consumption increases along with maximum aerobic speed. The increase in maximum aerobic speed with temperature is reduced somewhat by an increased cost of locomotion. The intercept of the oxygen consumption vs. speed

function increases with temperature, even though the slope of the function (that is, the minimum cost of transport) tends to change less. At the highest temperatures, maximum oxygen consumption is reduced along with metabolic cost so that maximum aerobic speed remains the same in cockroaches (209) or decreases in ghost crabs (211, 500).

Dehydration

Dehydration, like temperature, can alter maximum aerobic capacity and endurance. Maximum aerobic speed in the ghost crab is reduced by 68% after losing only 3.6% of its weight in water (501). Rapid dehydration results in a larger decrease in maximal oxygen consumption than more gradual water loss.

Intermittent Locomotion. Most studies linking endurance to metabolism have focused only on constant speed, continuous locomotion. Few invertebrates move at a constant speed for long periods. Instead, most start and stop, move intermittently. Studies on ghost crabs

comparing intermittent and continuous locomotion show that performance limits are altered by movement pattern, even when the crabs walk at the same average work output or speed (499). Alternating intense exercise (that is, above the maximum aerobic speed) with rest pauses can increase or decrease the total distance traveled before fatigue (that is, distance capacity) depending on the duration of exercise and pause periods. Despite the fact that ghost crabs reach their maximal oxygen consumption at slow walking speeds, distance capacity can be increased by nearly twofold if the crabs run twice as fast but rest half the time (2 min exercise/2 min pause) compared with an individual exercising continuously at the same average speed. Given the appropriate intervals of intermittent locomotion, ghost crabs can reduce their relative metabolic work load from 84% to 68% of maximum oxygen consumption and effectively increase maximum aerobic speed (211). Use of other intervals can significantly reduce distance capacity compared to continuous locomotion at the same average speed.

The study of intermittent locomotion is a promising area for future research because it shows that dynamic physiological adjustments are likely to alter a system's performance. Characterization of the physiology of intermittent activities should produce a reevaluation of system functions (respiration, circulation, and muscle energy supply) with respect to transitions since most systems have been studied in the steady-state paradigm, where the focus has been on maximal capacities alone.

Temperature

Changes in temperature alter distance capacity during intermittent locomotion. Distance capacity during intermittent locomotion at low temperatures, where aerobic capacity is limited, can be comparable to an animal moving continuously at a body temperature 10° warmer (498, 499). These differences may be a result of temperature's effect on physiological rate processes during frequent pause-to-exercise and exercise-to-pause transitions.

Metabolic Cost of Transport

Engineers in 1950 devised a dimensionless ratio called specific resistance that normalizes the energy cost of locomotion to allow comparisons among means of transportation. Specific resistance is defined as the metabolic cost per time divided by speed and weight (215). This index was applied to animals 20 years later and termed the cost of transport, the amount of energy used to move a unit mass a unit distance (463, 478). The index is useful because it allows comparison of diverse species and can be ecologically relevant since

animals move known distances and for particular amounts of time.

Speed. The total cost of transport varies with speed. Values used for comparison are typically the net [(active oxygen consumption—resting consumption) / speed] or the minimal (slope or tangent of the oxygen consumption vs. speed function) values at whatever speed this is attained (192). Net and minimal values remove the metabolic cost of resting.

Running and Crawling

The total cost of transport in crawlers (54, 97, 277, 292), walkers, and runners (192) declines with an increase in speed. The decline is a result of the resting consumption and the y intercept (when elevated above resting consumption), contributing a substantial proportion to the total costs at low speeds but less so at high speeds. The majority of species attain 80% of the minimum cost at the fastest sustained speed. The actual minimum cost of transport is equal to the slope of the oxygen consumption vs. speed function.

Swimming

The total cost of transport in swimming shrimp (244) and small blue crabs (276) attains a minimum at intermediate speeds. Since oxygen consumption increases curvilinearly with speed, the minimum is estimated by the slope of a line from zero tangent to the curve. Underwater walkers (276, 278, 280) and swimming euphasids (468) show a total cost of transport function similar to that of runners and crawlers.

Flying

In the only study of metabolic cost during quantified forward flight, the rate of oxygen consumption does not vary with flight speed (173). Therefore, the total cost of locomotion per distance decreases with increasing speed. Estimates of the minimum cost of locomotion have used flying speeds that range from preferred speed to the highest sustainable speed. The lack of measurements and the uncertainty about the position of a minimum for comparison, if one exists, make the data set for flying the weakest.

Size

Running

The mass-specific minimum or net cost of transport for runners decreased by 20-fold over four orders of magnitude in body mass [(191, 192); Table 12.4 Fig. 12.13]. Small runners, such as ants, use far more energy to move a gram of their body 1 m than do large invertebrates, like crabs.

Swimming

Body mass has a substantial effect on the mass-specific cost of transport in swimmers (Table 12.4; Fig. 12.13). The mass-specific cost of transport for the largest swimmers is only one-twelfth that of the smallest invertebrates, which are five orders of magnitude smaller in mass.

Flying

The mass-specific cost of transport for flight does not change significantly with body mass (Table 12.4; Fig. 12.13). The trend is the same as in running and swimming but possibly with a shallower slope. This is primarily a result of the lack of data. Although many studies have been conducted on hovering (zero speed), only one study to date has measured the cost of transport in forward flight (173).

Mode of Locomotion. Swimming is the most economical mode of locomotion over five orders of magnitude in body mass. Swimmers use less energy per time than runners but move at similar speeds (Fig. 12.13). Swimmers include species that move by rowing, undulating, and walking under water because no significant differences were found between these groups. Aquatic jet propulsion in squid and jellyfish is as economical as other modes of swimming. All of the swimming data are consistent with the hypothesis that reduced gravity may decrease energy cost.

Burrowing worms of approximately 3 g use 80 times the energy required by swimmers to move a unit mass a unit distance and 22 times that of a runner. Burrowing is the least economical mode of locomotion partly due to the high resistance of the medium. Three-gram crawlers use 22 times the energy of swimmers and six times the energy of runners of a comparable mass. Burrowing worms and crawlers, including snails, slugs, and insect larvae, use far more energy than runners and fliers. Burrowers and crawlers use hydro-

static skeletons, whereas runners and fliers use jointed framework skeletons. The supportive role of hydrostatic skeletons may result in hydrostats requiring greater force production and energy expenditures than animals using jointed framework skeletons.

Fliers have the highest metabolic cost of locomotion per unit time but travel the fastest (Fig. 12.3), thus reducing the cost of transport to equal to or below that of runners. A 1 g flier uses half the energy of a runner, but over twice that of a swimmer, to move its body 1 m. Because mass-specific metabolic cost per time increases more in small runners than in fliers or swimmers, a 1 m flier uses one-third of the energy of a runner but 1.7 times that of a swimmer. A 1 g runner uses twice the energy required by a flier and four times that of a swimmer, whereas a 1 mg runner uses three times the energy required by a flier and five times that of a swimmer to move its body 1 m. Fliers and runners must still generate force to overcome gravity, whereas its effect in swimmers is reduced.

Species*Running*

Two taxonomic groups stand out from the other runners with respect to cost per distance when the effects of body mass are removed: cockroaches tend to have the highest mass-specific cost of transport (259) and centipedes and millipedes fall at the lower end of the transport cost distribution (212). No significant trends are found for beetles, ants, crabs, and crickets, but one species of ant, *Pogonomyrmex rugosus*, does show a rather low cost per distance (342, 346).

Swimming

Jetting squid have been hypothesized to have a high cost of transport because they must generate thrust by pushing small volumes of water at high speeds compared to fish which push a large volume of water back slowly with their tails (510). Molluscs may be limited

TABLE 12.4. *Scaling of the Cost of Transport as a Function of Body Mass*

Mode	Name (Taxonomic Group)	Cost of Transport (ml O ₂ ·kg ⁻¹) = $a m^b$			r	n	P
		Mass Range (kg)	b (S.E.)	log a (S.E.)			
Runners	All	0.0000047–0.166	–0.334 (0.039)	–0.338 (0.126)	0.83	35	<0.001
Swimmers	All	0.00001–0.905	–0.248 (0.065)	–0.683 (0.208)	0.76	13	0.003
Fliers	All	0.000002–0.002	–0.126 (0.079)	0.020 (0.353)	0.52	9	0.154

by their cavity volume. Yet, the cost of transport in jetting molluscs is not significantly different from that of swimming crustaceans of the same mass. Multiple paddle systems used by rowing crustaceans have also been hypothesized to be a more costly mechanism of locomotion than undulatory swimming by fish (467). Two species of shore crab and lobster walking under water have transport costs comparable to those of other swimmers (278). The shore crab *Carcinus maenas* is an exception and has a cost of transport comparable to that of a runner, despite the fact that in water it weighs one-tenth its weight in air (276, 280). Additional research comparing walking under water and in air is needed to determine the basis for differences. Obvious alterations in kinematics exist in some species. For example, crayfish can walk twice as fast under water by doubling stride frequency [weight drops by two- to three-fifths (410)]. Small hydromedusae jetting jellyfish have costs of transport similar to those of other swimmers (130). By contrast, scyphomedusae jellyfish have been reported to have one of the lowest costs of transport on record (338). Jetting salps may have even lower transport costs (474). Both species attain their speeds with 1% or less of their body mass devoted to locomotor muscle.

Crawling

The cost of transport for snails crawling on land is approximately twice that of those crawling in water, but values from both media are high compared to other species of a similar mass (277). Crawling insect larvae (54, 97, 267) have a higher cost of transport than snails using pedal waves on land.

Flying

All that can be said of the measurements for flying is that the most reliable cost of transport value is high and falls nearest to the regression line for runners. Bumblebees use about 5 ml O₂/kg⁻¹·m, or about 100 W/kg⁻¹·m (173).

Temperature. The minimum cost of transport is surprisingly temperature-insensitive when diverse taxonomic groups are surveyed. In general, the same is true within a species. Most of the available data have been collected on runners. Herreid et al. (263) were the first to show that the cost of transport was independent of temperature by exercising the Madagascar hissing cockroach on a treadmill. The y intercept of oxygen consumption vs. speed function can increase with temperature, but the function's slope does not vary. The minimum cost of transport in large *Blaberus* cockroaches does not vary with a temperature change from 15° to 34°C (209), nor does it change in ants from 34°

to 43°C (346). The minimum cost of transport decreases in ghost crabs at the highest body temperatures used (30°C) (211, 500). The lower cost of locomotion results in a greater endurance because the maximal oxygen consumption, though reduced, is not attained until higher speeds.

CONCLUSIONS

The broad picture of locomotion in invertebrates is one of strikingly general patterns within the context of rich and impressive diversity. Numerous models of function and new concepts have come directly from examination of this diversity: novel lift-generating mechanisms in aerodynamics, unexplored concepts for the design of walking robots (for example, leg design and joint moment minimization), unique biomaterials that await application, and new approaches to hydrodynamics (for example, at intermediate Re's) are just a few examples. Direct experiments on a restricted set of species, especially ones more like ourselves, could never result in the large differences in structure and function observed due to mode of locomotion, body mass, or species differences. Without a consideration of diversity, discoveries and conclusions would necessarily be limited.

With this diversity comes the challenge of generalization. There is no large taxon or mode of locomotion well represented by any one model and a few regression lines. There is no one wingbeat frequency for a flier of a given body mass, no single speed for a swimmer, and no one value for the cost of transport of a runner. An extraordinary spectrum of capacities exists, as shown by the range of values and the number of distinct relationships. The study of invertebrate locomotion provides a striking example of how comparing a handful of species that differ in body mass or form can result in only the most tentative, general, conclusions.

The strength of general conclusions from natural experiments is dependent upon selecting the appropriate species for comparison. Uncertainty due to the "missing experiment" or the lack of a proper control for comparison becomes paramount in importance. Data sets are most often incomplete and have interactions that cannot be easily separated by comparison of selected species. For example, as far as we know, the highest sustained power outputs of invertebrates are generated only by fliers. All invertebrate fliers are insects. It is difficult to say how much of this capacity is due to the special properties of insect muscle, the temperature at which they operate, the musculoskeletal system mechanics, the effective respiratory system, the biochemical pathways involved, and so on. It would

be preferable to have a natural experiment in which nearly identical species differed only in muscle properties or temperature or musculoskeletal function or oxygen delivery or the biochemical pathway utilized. If these appropriate subjects for the natural experiment cannot be found or produced by genetic manipulation, one must rely more on direct experiments on isolated muscles and skeletons, which may disrupt the complex functioning system in unforeseen ways. Alternatively, one could examine many species and control for differences by considering phylogeny (see the chapter by Bennett in this *Handbook*).

Data sets comparing taxonomic groups are seldom selected at random and, therefore, may be biased. A truly random selection, which is desirable in a statistical sense, may not be the most appropriate. For example, if by chance one selected a species of small butterfly, a medium-sized dragonfly, and a large bee, wingbeat frequency in insects would appear to increase with body mass (Fig. 12.4). If one selected only flower flies, no relationship would be found. Yet, within most groups wingbeat frequency clearly decreases with body mass. Selection of groups for comparison must be based on the evolutionary relationships of the groups with respect to the diversity present in the variables of interest (see the chapter by Bennett in this *Handbook*). Unfortunately, these relationships are not always available. Also, selection by conventional taxonomic groupings is not necessarily accompanied by equivalent diversity in the variables of interest. Sometimes comparisons of families are appropriate, whereas in other instances species must be examined. The probability that another variable will confound a natural experiment is decreased by a wise selection of species, just as it is by the selection of the appropriate control in a direct experiment.

Recognizing the challenge of understanding the remarkable diversity in invertebrate locomotion, one is best served by partitioning the variation with the fewest variables necessary to represent the largest possible taxonomic group of interest. To accomplish this, one proposes hypotheses of function that are the simplest and most general. General quantitative models of function are essential for rapid progress but should be considered as standing hypotheses and should not discourage future testing. More importantly, the general relationships among variables from one or a few taxonomic groups that test models should be considered in most cases as only a single test of the general model. General models can become more or less broadly applicable with the next data set. Moreover, the next data set may result in the rejection of one general model and the development of another.

Upon partitioning the extraordinary variation seen in

invertebrate locomotion, equally extraordinary general patterns are observed: the striking similarities in scaling of speed, cycle frequency, power output and input, oxygen consumption, and the cost per cycle with body mass; similarities between runners and swimmers in speed, cycle frequency, and power output; the remarkable capacity of fliers; the comparable cycle distance for all species; the high cost of locomotion in hydrostats; and the low cost of swimmers are just a few examples. Given the preceding caveats, I present hypothesized links between comparative bioenergetics, muscle physiology, and the biomechanics of invertebrate locomotion to support these general relationships. Further work is necessary to test these hypotheses within a phylogenetic context.

Trends

Speed, Cycle Frequency, and Cycle Distance.

Body Mass

Speed tends to increase only moderately with body mass for all modes of locomotion (Figs. 12.3, 12.14H). A greater scaling effect may be present within taxonomic groups than between them. Small animals attain speeds closer to large animals by cycling their propulsive units (wings, legs, bodies, or undulatory body waves) more frequently (Figs. 12.4, 12.4B), despite the fact that small animals travel a much shorter distance per cycle (Fig. 12.14E). The distance traveled per cycle scales nearly as predicted from geometric similarity ($m^{0.33}$).

Mode of Locomotion

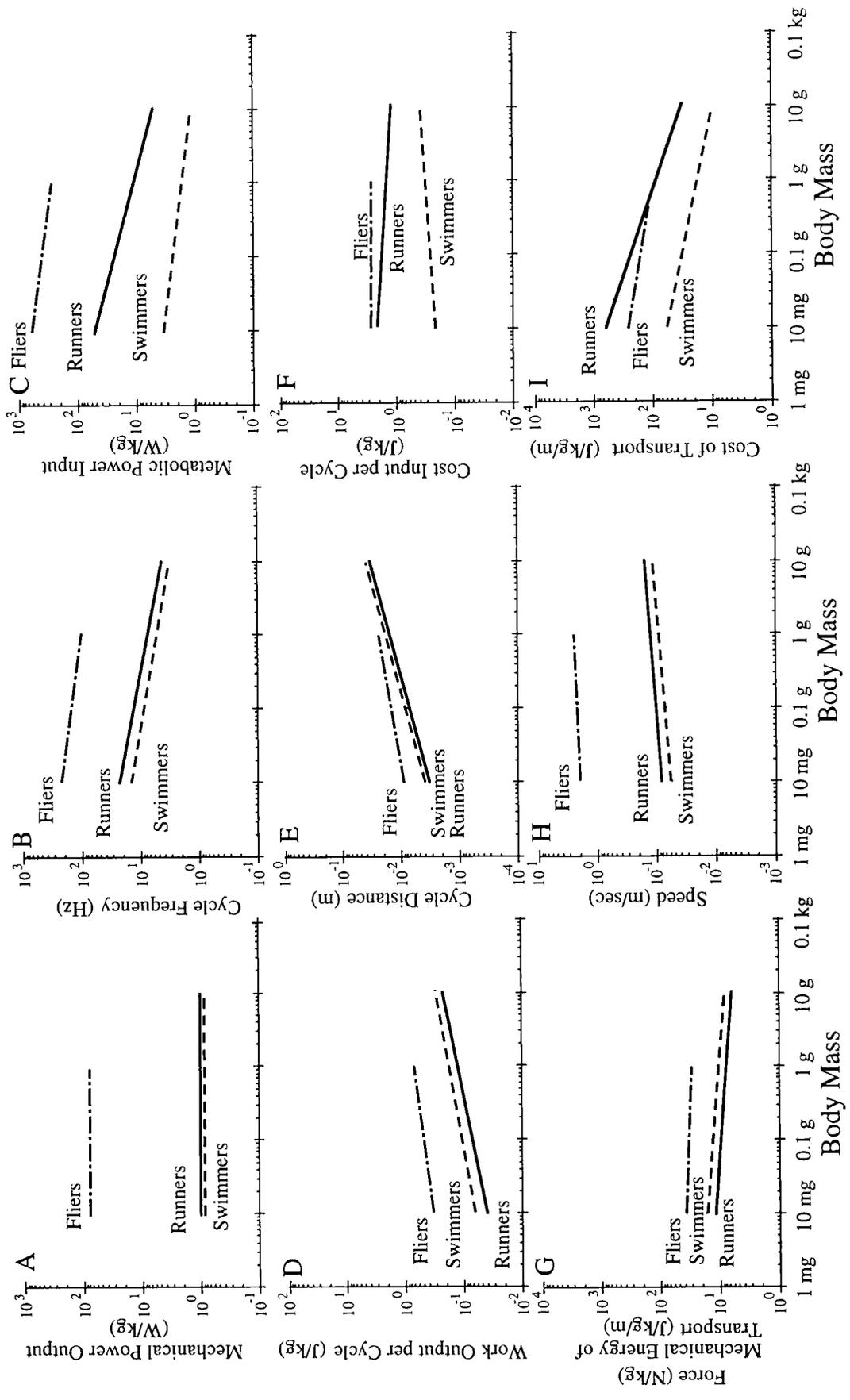
Differences in the distance traveled per cycle among the modes of locomotion are small. Fliers are faster than runners and swimmers because they beat their propulsive units at extraordinary frequencies.

Mechanical Power Output

Body Mass

Invertebrates appear to generate mechanical power in direct proportion to body mass to attain the speeds observed. The whole-body, mass-specific mechanical power output produced is independent of body mass (Figs. 12.5, 12.14A). More data are certainly required for all groups. The evidence for the independence of mass-specific mechanical power output from body mass is strongest in fliers and weakest in runners and swimmers. Mass-specific mechanical power output may even increase with body mass in fliers.

High cycle frequency is a major reason that small animals can have mass-specific mechanical power out-



puts comparable to large animals. Mass-specific mechanical power output is relatively independent of mass because cycle frequency increases with a decrease in body mass, whereas mass-specific work per cycle is less in small animals (Fig. 12.14A equals cycle frequency times work output per cycle, 12.14B · 12.14D). Since the equivalent mechanical forces developed in small and large animals are more similar (Fig. 12.14G), mass-specific mechanical work per cycle is less in small than in large animals because small animals travel a shorter distance per cycle (Fig. 12.14D, equals 12.14G · 12.14E).

Mode of Locomotion

Although fliers vary in mechanical power output, the rates are one to two orders of magnitude greater than in runners and swimmers (Fig. 12.5). No difference can be discerned between runners and swimmers. The greater mechanical power output of fliers compared to swimmers and runners is a result of a 20- to 30-fold greater cycle frequency and a three- to six-fold greater work output per cycle (Fig. 12.14A, equals 12.14B · 12.14D). Work output per cycle is a function of the distance traveled per cycle and the equivalent force developed (Fig. 12.14D, equals 12.14E · 12.14G). Fliers and fast runners may have somewhat higher cycle distances than slower animals, thereby increasing work per cycle (Fig. 12.14E). In addition, fliers may have to generate higher equivalent mechanical forces (Fig. 12.14G). A 0.1 g flier may exert twice the equivalent force of a swimmer and three times the force of a runner to produce the profile and inertial power necessary for flight (Fig. 12.14G). The equivalent force for a 0.1 g animal is equal to 3.6 G's (gravitation force) for fliers, 1.4 G for swimmers, and 1.0 G for runners.

A major area of uncertainty in integrating whole-body mechanical power output to muscle mechanical power output in flying, swimming, and running is the extent of elastic strain energy storage by musculoskeletal units. If more mechanical energy can be stored and returned by the musculoskeletal unit, then lower power outputs are required from the muscle itself. If the

ability to store elastic strain energy changes with body mass, then whole-body mechanical power output will not reflect muscle mechanical power output. If the contribution of elastic strain energy storage is greater in larger invertebrates, then mass-specific muscle mechanical power output would be decreased at larger masses. The data available for mass-specific muscle mechanical power output using the work-loop technique support the hypothesis of mass independence (Fig. 12.8A), but elastic structures demand more attention.

Metabolic Power Input

Body Mass

Whole-body, mass-specific metabolic energy input derived from the oxygen consumption data decreases with body mass in contrast to mechanical energy output (Fig. 12.11, 12.14C). The scaling of mass-specific metabolic power input results from the scaling of cycle frequency since mass-specific metabolic cost per cycle is nearly independent of body mass (that is, per wingbeat, stride, stroke, or wave; Fig. 12.14F). Available data are sparse, but mass-specific cost per cycle values of fliers, runners, and crawlers support this trend (Fig. 12.15). The mass-specific cost per cycle of a 2 mg mosquito is the same as that for a 30 g crab. For synchronous fliers that vary widely in morphology or oxygen consumption rates, mass-specific metabolic energy per stroke is independent of body mass (96). A similar trend is seen within asynchronous fliers, but the energy cost per stroke is somewhat less. The metabolic power input of sphinx moths and euglossine bees follows the same scaling function. Sphinx moths operate at lower wingbeat frequencies (25–66 Hz) compared to euglossine bees (80–240 Hz) over the same range of body masses (102). Therefore, the cost input per stroke in sphinx moths is 12–25 J/kg, whereas the value is 3–4 J/kg for euglossine bees of the same mass (0.6 g). Casey (98) noted that these differences parallel those of muscle strain. Strain of synchronous fliers is near 6%, whereas the values for asynchronous muscle

FIG. 12.14. Hypothesized relationships of invertebrate locomotion based on literature review. *A*: Mass-specific mechanical power output (see Fig. 12.5), the product of cycle frequency and mass-specific mechanical work output per cycle. *B*: Cycle frequency (see Fig. 12.4). *C*: Mass-specific metabolic power input (see Fig. 12.11), the product of cycle frequency and mass-specific metabolic cost input per cycle. *D*: Mass-specific mechanical work output per cycle, the product of cycle distance and mass-specific mechanical work output per cycle, the product of cycle distance and mass-specific resistive force or mass-specific mechanical energy of transport. *E*: Cycle distance. *F*: Mass-specific metabolic cost input per cycle (see Fig. 12.12), the product of cycle distance and mass-specific metabolic cost of transport. *G*: Mass-specific resistive force or mass-specific mechanical energy of transport. *H*: Speed (see Fig. 12.3), the product of cycle frequency and cycle distance. *I*: Mass-specific metabolic cost of transport (see Fig. 12.13).

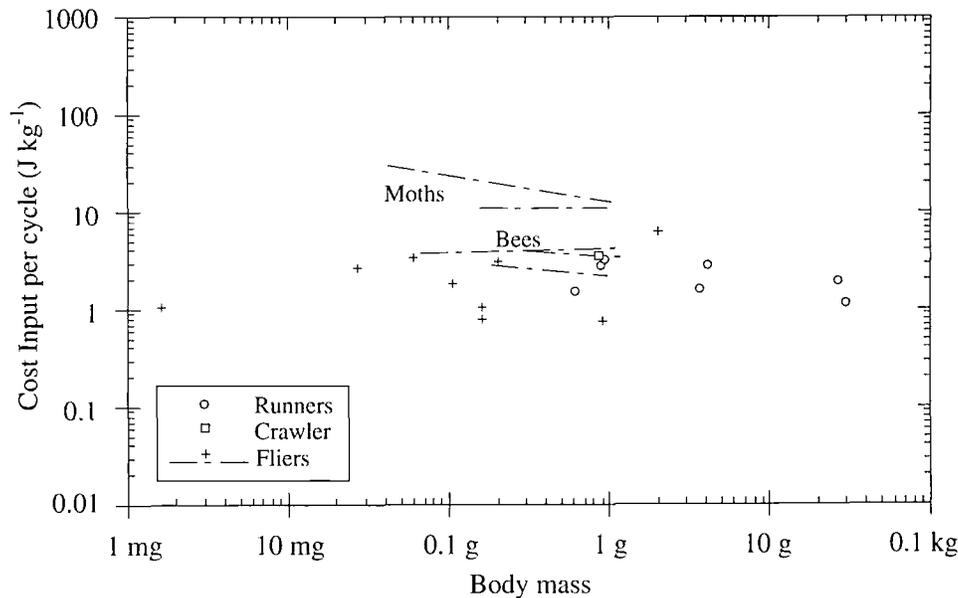


FIG. 12.15. Mass-specific metabolic cost input per cycle as a function of body mass. Regression lines represent a range of body masses for a given species. Data include runners (22, 190, 209, 210, 212, 261), a crawler (97), and fliers (42, 251, 273, 447, 502, 507) such as moths (96) and bees (96, 102, 521).

are closer to 1%–2% of resting length. The metabolic cost input per stride in running 1 g insects ranges from 1.5 to 3.1 J/kg (212). A 1 g crawling moth larva uses 3.6 J/kg (97), whereas cockroaches, four times as massive, have values of 2.7 J/kg (209) and ghost crabs 27 times as large use 1.9 J/kg (69, 190). Mass-specific metabolic cost per cycle is independent of body mass because the greater mass-specific cost of transport of small animals is offset by the shorter distance traveled by small animals in a cycle (Fig. 12.14F equals $12.14I \cdot 12.14E$).

Mode of Locomotion

Fliers require by far the greatest metabolic power input. The metabolic power input of some runners and swimmers approaches that of fliers for short periods with the aid of nonaerobic metabolism. Runners require far more metabolic energy per unit time than swimmers, whereas they appear to generate similar amounts of mechanical power to move. Whole-body efficiencies for invertebrates increase with body mass for all modes of locomotion. For body masses of 10 mg to 1 g, whole-body efficiencies range 12%–38% in fliers, 2%–20% in runners, and 21%–67% in swimmers. Whole-body efficiencies may not reflect muscle efficiencies because of the uncertainty concerning the amount of elastic strain energy storage and energy transfer (192). The high whole-body efficiencies at the largest body masses point to the strong likelihood of significant contributions from elastic storage. The

efficiency of fruit fly flight has been estimated to be near 10% (148). Cockroaches running on inclines have efficiencies of 3%–4% (210). The only estimate of invertebrate muscle efficiency using the work-loop technique gives values of 4%–10% for the flight muscle of a 1.6 g locust (316). Josephson and Stevenson (316) found that the metabolic cost of positive work, isometric contractions, and negative work varied by less than 15% and concluded that the extra costs of shortening and doing external work are not very large compared to isometric costs, which represent the energy needed to cyclically activate the muscle.

The large difference in metabolic power input between fliers and swimmers may be explained in part by the extraordinary difference in cycle frequencies (Fig. 12.14B,C). When cycle frequency is considered, variation in the metabolic cost input per cycle (based on calculated regressions; Fig. 12.14F) among fliers, runners, and swimmers is only tenfold compared to the 1,000-fold variation in metabolic power input (Figs. 12.11, 12.14). Swimmers appear to have the lowest metabolic cost per cycle (Fig. 12.14F) because of their exceptionally low cost of transport (Fig. 12.14I).

Explanatory Hypotheses of Trends

Body Mass

Because the propulsive units (wings, legs, bodies, or undulatory body waves) of small invertebrates cause them to travel a shorter distance per cycle than larger

invertebrates, small invertebrates must cycle their propulsive units more frequently to attain speeds more similar to larger animals. If small animals swept their propulsive units through the same angles as large animals and had a similar mechanical advantage, then their muscles would be shortening with similar strains. If the muscles of small invertebrates were to undergo strains comparable to large animals, then the muscles of these smaller animals would have to contract at speeds near v_{\max}^M or above. Instead, in smaller invertebrates, an increase in cycle frequency appears to be accompanied by a decrease in muscle strain (Fig. 12.8). A reduction in muscle strain without a change in mechanical advantage should result in a shorter cycle distance. Small invertebrates, however, appear to have smaller mechanical advantages [in-lever to out-lever arm ratios (r/R)] relative to larger animals. Smaller in-lever arms result in velocity amplification at the expense of force or moment production. Small animals with muscles generating force over small changes in length could have shorter sarcomeres than larger animals. If small invertebrates had shorter sarcomeres than large animals but similar relative fiber lengths, then a greater strain rate could be attained for a given interfilamentary velocity because of the greater number of sarcomeres in series.

The short time period which small invertebrates have to produce force has major consequences. To produce adequate power in a short period, muscles must be activated and relaxed as rapidly as possible. If the muscle does not completely relax before the start of the next power stroke, negative work will be done on the muscle to relengthen it. If the muscle is not activated before the start of the power stroke, the reduction in force will lead to a lower work per cycle. Even if stimulation does occur during the end of the recovery stroke, force may still be compromised due to variable activation, shortening deactivation, or stretch effects. Muscle stress and work per cycle could decrease for animals with smaller body masses (or higher cycle frequencies; Figs. 12.8, 12.14D). Mass-specific power output is not lower in small animals compared to large because small animals use very high cycle frequencies.

The high cycling frequencies used by small invertebrates necessitate that muscles generate force and do work at very high rates. Small animals must recruit faster fibers with greater v_{\max}^M values that have high rates of ATP utilization at all contraction velocities and are less economical (force generation relative to ATP breakdown) than slower fibers. The rapid relaxation rates necessary for power output in small animals require high rates of calcium cycling by the sarcoplasmic reticulum and, therefore, high rates of ATP breakdown. When segment cycling period is considered, the

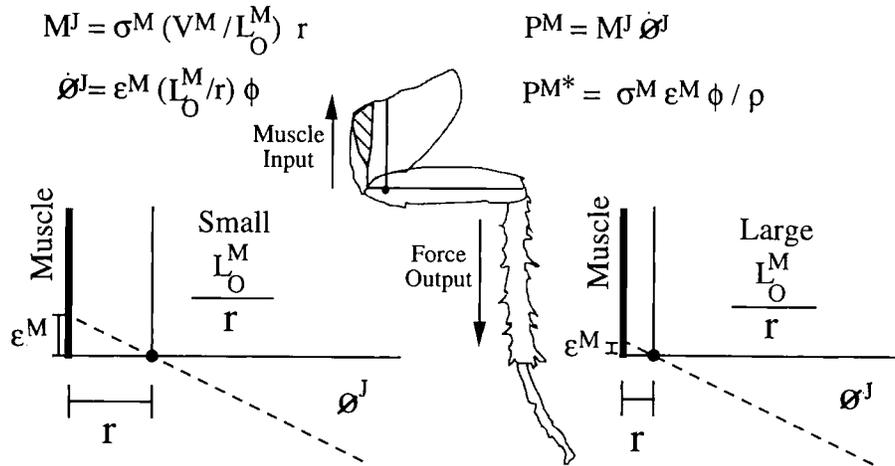
mass-specific metabolic cost per cycle is similar for small and large invertebrates using a given mode of locomotion.

Mode of Locomotion

Hypotheses similar to those proposed for scaling can be applied to explain variations in mechanical and metabolic variables resulting from differences in mode of locomotion for animals of the same body mass (Fig. 12.16). To attain high speeds and to generate high mechanical power outputs, fliers and exceptionally fast runners cycle their propulsive units at high frequencies (Figs. 12.4A, 12.14B) but travel distances in one cycle more similar to those of slower animals (Fig. 12.14E). Similar cycle distances should correspond to propulsive units swinging through like angles. If fast invertebrates sweep their propulsive units through angles that do not differ greatly from those of slower animals and muscle strain is lower at high frequencies (Fig. 12.8; see equation 12-31), then the in-lever arms of fast invertebrates must be relatively short (decreased r) compared to the out-lever arms (R ; that is, a lower mechanical advantage but greater velocity amplification). Fast invertebrates, such as insect fliers, have shorter sarcomeres that generate force over narrow strain ranges (Figs. 12.7, 12.8). If fast animals have fiber lengths similar to those of slower animals, then a greater muscle velocity could be attained for a given interfilamentary velocity because of the greater number of sarcomeres in series.

As in small animals, the short cycle periods found in faster animals can result in lower muscle stress and work output per cycle because of the difficulty in rapidly activating and relaxing the muscle. Work loops in faster animals tend to be more ellipsoid compared to the more rectangular shape in slower animals (Fig. 12.9). Faster animals tend to generate greater power outputs.

The high cycling frequencies in fast animals are associated with faster fibers, which are more metabolically costly because of rapid ATP breakdown by the cross-bridges and sarcoplasmic reticular calcium pumps. Rapid calcium cycling in fast muscles is generally associated with a greater amount of sarcoplasmic reticulum and, therefore, a possible reduction in myofibril or contractile tissue volume. Van Leeuwen (480) has argued that the highest power outputs should be from animals that have short sarcomeres, operating with small strains and possessing few mitochondria and little sarcoplasmic reticulum. Asynchronous fliers operating muscles by stretch activation nearly meet these predictions, except that they can sustain flight and, therefore, have considerable amounts of mitochondria.



	Low Power Output	High Power Output
Mass	Similar	Similar
Speed	Low	High
Cycle frequency— ϕ	Low	High
Cycle distance	Equal	Equal
Angle— θ^J	Equal	Equal
Muscle strain— ϵ^M	Large	Small
In-lever arm— r	Long	Short
Sarcomeres	Long	Short
Muscle contraction & relaxation rates	Low	High
Muscle Stress— σ^M	Increased	Reduced
Work-loop shape	Rectangular	Ellipsoid
Rate of ATP breakdown	Low	High

FIG. 12.16. Trends for variation in power output. Two hypothetical animals of the same mass are compared. The morphology of a hypothetical appendage is shown to illustrate mechanical advantage, muscle strain, and the angle swept by the appendage. *Left column* represents trends for an animal that generates lower power output than the animal represented at *right*. Equations show how variables (muscle moment, joint angle, and muscle power output) are used to derive mass-specific muscle power output (P^{M^*}). See text for explanation.

Cycle frequency—related variables alone are not sufficient to explain the metabolic cost differences between flying, swimming, and running. Despite the fact that the mechanical work output per cycle is similar in runners and swimmers of the same body mass (Fig. 12.14D), metabolic cost per cycle may be significantly

greater in runners (Fig. 12.14F). The difference is likely due to supporting the body's mass against the force of gravity. Runners repeatedly accelerate their body because after each acceleration gravity pulls them back to the surface and as legs contact the ground they produce a deceleration (that is, muscles absorb energy

and do negative work). Even though runners may operate as spring-mass or pendulum systems, leg springs are not simply passive structures; therefore, leg muscles must still be activated to provide an acceptable stiffness to operate a resonating system. Running cockroaches generate substantial amounts of force with all legs, despite the fact that ground reaction force vectors are aligned along the leg, minimizing joint moment (211). Force production alone costs metabolic energy, but it is not reflected in mechanical energy.

Swimmers may have lower costs per cycle because less muscle force is necessary since they do not repeatedly support their air weight and stabilize appendages against gravity to maintain the body's position. Likewise, negative work may be reduced during swimming so that less muscle force production is involved in energy absorption. A third possibility is that the force developed during positive work production in swimmers is developed over a longer period of the cycle time than during running (that is, equivalent to a longer duty factor), thereby reducing the cost of force production. Crabs and lobsters walking under water appear to use less energy per distance than terrestrial crustaceans (276, 278, but see 280). Snails use twice as much energy when crawling on land compared to crawling under water (277).

FUTURE RESEARCH

Extraordinary progress has been made in the areas of comparative bioenergetics, muscle physiology, functional morphology, and biomechanics, but there is much to be done. Future studies must explicitly continue the attempt to *integrate* these areas (Fig. 12.1).

Comparative Muscle Physiology

Research which attempts to replicate the operation of the muscle in the animal (311, 361) has shown that it is time to move beyond cursory efforts to demonstrate how another muscle might be optimized for power output according to the Hill model and its steady-state, isotonic force–velocity curve. Direct application of the steady-state, isotonic force–velocity curve has been called into question by studying scallops and locusts (354, 361) with respect to degree of activation. Moreover, muscles have been found that absorb energy only during terrestrial and aerial locomotion (3, 477).

Muscle and its associated skeletal elements have extraordinary properties. Musculoskeletal actuators must be considered to be integrated units which have properties of springs, dashpots (viscous, energy-dissipative elements) (375), and neurally controlled force generators all at the same time (529). A musculo-

skeletal complex at times can be a spring when force output depends only on its length, a dashpot when force output depends only on its velocity, or an independent, neurally controlled force generator when force output depends only on its neural input and activation dynamics. Even though these properties have been modeled or studied in isolated muscle preparations, in multiple muscle systems their consequences to organismal level function clearly deserve more attention. The challenge ahead will be to discover how multiple muscles work in concert to allow animals to swim, crawl, jump, fly, run, and even roll (Fig. 12.1B). A synthesis between comparative muscle physiology and locomotor biomechanics is essential.

Comparative Bioenergetics and Exercise Physiology

Research on locusts has shown that it is possible to measure the energetics and mechanics of muscle at the same time (316). Studies in comparative biomechanics have demonstrated that data about muscle function in the animal can be obtained from dynamics (kinematics—motion and kinetics—forces) and used by comparative muscle physiologists to mimic conditions during locomotion (3, 222, 362, 477). These studies indicate that it is time to move beyond measuring the cost of locomotion in another species. If mechanistic questions are to be answered about the cost of locomotion, then a synthesis between comparative bioenergetics and locomotor biomechanics is essential (148).

It is also time to move to the next step in defining performance limits as they relate to comparative bioenergetics. Animals seldom swim, run, and fly at a constant speed under invariant conditions. Instead, they locomote intermittently against wind and waves and over and around complex terrain. Research has shown that intermittent locomotion can alter performance limits compared to constant speed locomotion (499). System functions (respiration, circulation, and fuel utilization) need to be re-evaluated with respect to the rapidity of transitions to complement the work on maximum steady-state performance. The energetics of maneuverability is an open area.

Comparative bioenergetics of locomotion could contribute much to ecological energy budgets in the future. Moreover, it is likely to have a major impact on applied research focusing on biocontrol agents.

Comparative Biomechanics

Quantifying the dynamics of locomotion is obviously essential if integration of bioenergetics and muscle function is to be achieved. Muscles and their associated skeleton function as an actuator which must work together with the dynamics of the body segments (529).

The force-generating capacity of an actuator is affected by its length and velocity, which in turn depend on the position and motion of the body segments (Fig. 12.1B). Body segment motion depends on the force of the actuator. Muscle, its skeletal attachment, and body segments comprise a truly coupled, multiple input–multiple output feedback system (529).

Unlike bioenergetics, more data on biomechanics are needed to quantify even constant speed, steady-state locomotion. Yet, in systems better described, future research on maneuverability will break important new ground. Comparative biomechanical data and data on maneuverability in particular, will continue to provide inspiration for the design of robots. Full (193) has worked with engineers to apply new ideas from insect running toward the design of hexapedal robots that may explore Mars (63). Joint ventures between biomechanists, engineers, and the private sector [for example, U.C. Berkeley, Rockwell International, and IS Robotics are collaborating on the design of autonomous, legged, underwater vehicles inspired from research on crabs (363)] should be encouraged and can benefit all.

What has facilitated, and will continue to facilitate, research in comparative bioenergetics, muscle physiology, and biomechanics?

Collaboration

The time is right for biologists to work more closely with engineers (for example, artificial intelligence, elec-

trical, mechanical, systems), mathematicians, and computer scientists. Biologists provide inspiration for the design of new devices and materials, whereas engineers, mathematicians, and computer scientists give us hypotheses of function and powerful quantitative tools to test them.

Direct-Experiments Using Innovative Technology

The ability to measure variables directly has greatly aided progress. New tools and techniques have allowed measurements to be made that were not possible previously or were simply too difficult or costly. Quantitative measures of locomotor variables can be collected by virtual instruments in software running data acquisition hardware. High-speed video for three-dimensional kinematics, telemetry, image analysis hardware and software, lasers, sensitive strain gauges and photoelastic gelatin slabs to measure force production, sonomicrometers to measure length, and extraordinarily sensitive O₂, CO₂, and H₂O gas analyzers are just a few of the tools at hand (59).

Cybercreatures and Experiments: Computer Modeling

In particular, musculoskeletal computer models that tackle three-dimensional complexity and the many parameters of each musculoskeletal complex (that is, muscle and its skeletal connection, such as an apodeme) will be invaluable in the future (195). Sensitivity and optimization analyses can be used to determine which

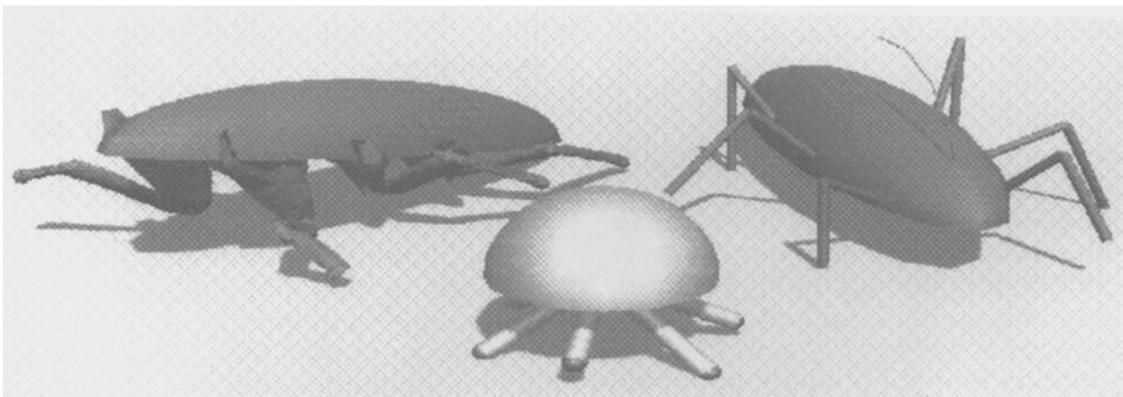


FIG. 12.17. Cyber-invertebrates. Dynamic models of legged animals designed by M. Raibert, MIT, and Boston Dynamics in collaboration with R. J. Full at U.C. Berkeley. Simulations consist of equations of motion, ground contact models, a numerical integrator, and a three-dimensional graphics program. All models obey the laws of Newtonian physics and are not simple kinematic representations. The Hexahopper (*center*) is an abstracted insect with telescoping legs attached to a hemispherical body. The model exhibits dynamic locomotion without an aerial phase as it bounces along. Three legs

act as one spring-mass system. The Hexabug (*right*) uses articulated legs attached to a long body. The legs have the length dimensions of cockroach legs. The Playback cockroach (*left*) uses the actual morphology of cockroach legs along with three-dimensional kinematics during running. The kinematic motion data can be played through the control system and the resulting dynamics analyzed. The controller uses the motion data to drive servos at each joint to apply moments which attempt to maintain target positions.

muscles and muscle parameters are particularly important. This information used in conjunction with direct experiments on isolated muscle that mimic function in the animal will result in the most rapid progress. In addition, computer models of limbs and whole bodies with representative three-dimensional dynamics that move in response to the net moments generated by the muscles spanning a joint will provide the link between isolated muscle dynamics and the transfer of energy to segments (Fig. 12.17). This approach will not only integrate muscle function with the biomechanics of the whole animal, but will also facilitate the integration of neural control.

Finally, we should agree with August Krogh, who at the Thirteenth International Physiological Congress in Boston in August 1929, commented on the advantages of selecting the most appropriate animal “I am afraid most of them are unknown . . . we must apply zoologists to find them and lay our hands on them” (332). Graham Hoyle (286) stated directly who these unknown animals are with respect to locomotion when he said, “Very small cold-blooded animals [invertebrates] with efficient nerve–muscle systems have, on the basis of total numbers, biomass, variety of habitats, and number of species, already inherited the earth.” Comparative bioenergeticists, comparative physiologists, functional morphologists, comparative biomechanists, and neurobiologists interested in animal locomotion have found, and will continue to *find*, invertebrates.

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APPENDIX: LIST OF SYMBOLS

*	mass- or length-specific
α	angle of pennation in muscle
A	area
A ^A	aperture area
A ^M	muscle cross-sectional area
AR	aspect ratio
A ^S	cross-sectional area of skeletal element
β	duty factor, fraction of time in a cycle that a leg <i>i</i> is in the support phase
b	retraction of leg, power, stance, or support phase
C _D	coefficient of drag
C _{dis}	coefficient of discharge in the thrust production of jettors
C _L	lift coefficient
C _{Lmax}	maximal lift coefficient
D	drag

D_{ind}	induced drag	μ	dynamic viscosity
D_{pro}	profile drag	M^J	moment about a joint
d	distance over which acceleration is generated in a jump	N	wing loading
ε	strain	n	number of legs
ε^M	strain in muscle	ϑ^J	angle through which the joint rotates
E_j	energy in a jump	$\dot{\vartheta}^J$	joint angular velocity
ϕ	cycle frequency	ϑ	angle of takeoff during a jump
F^A	connective tissue (e.g. apodeme) force	P	power
F_j	force generated during a jump	p	protraction of a leg, return, recovery or swing phase
F^M	force production of muscle	P^M	instantaneous muscle power output
F_o^M	maximum isometric force developed by muscle	P_{para}	parasitic power
F^S	segmental or skeletal force	Q	flow rate through funnel of jettors
F_{vert}	vertical ground reaction force at midstance	q	fraction of elongated or non-anchored segments in crawlers
g	acceleration due to gravity	θ	glide angle relative to the horizontal
g_f	gait formula for an n-legged animal where $g_f = (\beta_1, \beta_2, \dots, \beta_n, \varphi_2, \varphi_3, \dots, \varphi_n)$	θ_{min}	minimum glide angle
η	hydrodynamic efficiency	R	perpendicular distance from the point of force development by a segment to the axis of rotation
h_{air}	height of jump in air	ρ	density
h_{vac}	theoretical height attained <i>in vacuo</i>	r	muscle's lever arm
J	advance ratio	$R\#$	right leg #
φ	phase, fraction of a cycle time a leg i leads or lags another leg	Re	Reynolds number
k_{rel}	relative stiffness of the legs	s	designation of or relating to a segment
k^S	leg spring stiffness	σ_{jet}	pressure developed in jettors
k_{vis}	constant which depends on shape and orientation at low Re	σ^M	muscle stress
L	lift	σ_o^M	optimal or maximum muscle stress
$L\#$	left leg #	σ^S	skeletal stress
L_{amp}	stroke amplitude of wing	T	thrust
L_j	jump range	t	time
L^M	muscle length	t_{cyc}	cycle period
L_o^M	optimal muscle fiber length for maximum force production	ν	kinematic viscosity
L^{myo}	myosin filament length	u	velocity
L^S	characteristic length	u_{jet}	velocity of jet stream in jettors
L_o^S	initial length of the skeletal structure	u^M	shortening velocity of muscle
L^{sar}	length of a sarcomere	u_{max}^M	maximum shortening velocity of muscle
L_{stride}	stride length, distance the center of mass moves in a cycle	u_o	take-off velocity of a jump
L^W	wing length	u^S	velocity of a segment to which a muscle is attached
m	body mass	u^W	speed of propagating waves
		\bar{u}^M	relative velocity or strain rate of muscle fiber
		V^M	volume of muscle
		Y	Young's modulus