13.1

AFRICAN ELEPHANTS: ENERGETICS OF WALKING IN A LARGE MAMMAL.
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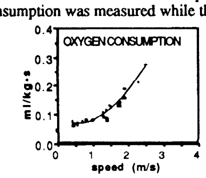
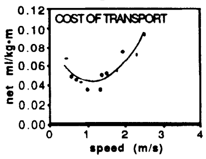
Elephants walk, but don't run. The muscles and bones of such large animals operate at stresses close to mechanical failure at top walking speeds, and switching to a run could have disastrous consequences. Their long limbs should let them walk rapidly at a low energetic cost, perhaps compensating for the single gait, and the purpose of this study was to to find out how fast they walk and how much it costs. Three female African elephants (ave wt. 1,540 kg) were trained to wear a gas mask and follow a motorized cart which carried air pumps, flow meters and gas collection bags. Oxygen consumption was measured while they walked at a constant speed for 5 minute intervals.





The net amount of oxygen used to transport each kg a meter (walking rate-standing rate divided by speed) reached a minimal value of 0.4 ml O2/kg•m at a speed of about 1 m/sec and doubled at both slower and faster walking speeds. Minimal cost of transport for the elephant was predicted remarkably well by allometric equations, and was 1/2 that of a pony and 1/4 that of a dog. Although minimal cost of transport differs by four-fold over this size range of dog to elephant, the speed where minimal cost was reached was nearly identical: a finding which we had not expected and brings into question the "pendulum paradigm" for explaining the link between energetics and mechanics of walking. This work was supported by NIH grant 5 RO1 AR18140-14.

13.2

THE IMPORTANCE OF REST PAUSES DURING INTERMITTENT EXERCISE IN THE GHOST CRAB, *OCYPODE QUADRATA*.
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Previous laboratory studies of animal locomotion have focused on the physiological responses to continuous treadmill exercise, yet most animals move intermittently. We have examined the importance of rest pauses by exercising medium sized ghost crabs (mean weight = 28.0 g) intermittently on a treadmill. Crabs exercised intermittently at 0.30 m/sec, a supramaximal speed twice the speed that elicits 75% maximal rate of oxygen consumption. When both the exercise and pause period durations were 120 sec, crabs exhibited a 6-fold increase in endurance compared to crabs exercised continuously at 0.30 m/sec and a 2-fold increase in endurance compared to crabs exercised continuously at 0.15 m/sec (a submaximal speed). In these crabs, lactate was cleared from the legs during the pause periods. When both the exercise and pause period durations were 30 sec, crabs exercised intermittently at 0.30 m/sec exhibited greater endurance than crabs exercised continuously at 0.30 m/sec, but not at 0.15 m/sec. In these crabs, lactate was not cleared from the leg during the pause periods and arginine phosphate levels remained low, but the 30 sec pause was sufficient to maintain constant ATP levels. Our results suggest that pause periods, if long enough, play an important role in clearing lactate and maintaining ATP levels in the leg muscles of intermittently exercised crabs. Supported by NSF Grant DCB89-04586 and an NSF Graduate Fellowship.

13.3

ENERGETICS OF UNDULATIONS IN CENTIPEDES.
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Lateral undulations have been hypothesized to significantly increase the cost of locomotion in animals using metachronal gaits. To test this hypothesis we exercised large twenty-two legged centipedes from Arizona (*Scolopendra heros*; 5.32 g ± 0.10 S.E.) on a treadmill enclosed in an airtight lucite respirometer. Oxygen consumption (V_{O_2}) was determined by open-flow respirometry. Flow rate was 240 ml/min. Speeds ranged from 0.16 to 0.74 km/h. Resting V_{O_2} was 0.22 ml O_2/g/h ± 0.004 S.E. O_2 consumption (ml O_2/g/h) *increased linearly* with speed (v, km/h); V_{O_2} =1.81 (±0.40 S.E.) v + 0.30 (r^2=0.67). Stride frequency and wave frequency (f, Hz) also increased linearly with speed (v, cm/sec; f = 0.13 v + 2.3, r^2=0.59). Based on the minimum cost of locomotion (1.8 ml O_2/g/km), cost per stride (1.8 J/stride) and ground contact cost (i.e. cost relative to the time a leg is on the ground generating force, 1.1 J/kg), we can reject the hypothesis that lateral undulation necessarily results in a considerable amount of "wasted energy" (Manton, 1953). In fact, when compared to all other pedestrian locomotors centipedes fall below the predicted costs for their body mass. Supported by NSF Grant DCP 89-04586.

13.4

DESIGN OF MUSCULAR SYSTEMS.
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The basic components of muscle contraction are understood and the ones that are varied (e.g., actin filament length, maximum velocity of shortening [V_{max}], and fiber orientation) can be considered design parameters. Are there rules (design constraints) that govern how these design parameters vary? Over the past 2 years we have identified two such constraints from studies on carp. A first constraint is the extent of myofilament overlap. Due to their helical orientation, the white muscle fibers have a 4-fold higher gear ratio than red ones. Hence, the white fibers can power the extreme "escape response" and the red ones power slow swimming, while each works at maximum overlap and force generation. A second important design constraint is V/V_{max} (where V is the shortening velocity of fibers). We know from isolated muscle experiments that maximum power generation and maximum efficiency are achieved over a narrow range of V/V_{max} values (.2 to .4). Carp power their slow swimming with red muscle (low V_{max}) and their fast movements with white muscle (high V_{max}) while each works within the optimal range of V/V_{max}. Further, if temperature is dropped by 10°C, the 1.6-fold drop in V_{max} of red muscle is matched by a 1.6-fold drop in maximum V (and swim speed), so that the muscle operates over the same V/V_{max} at each temperature. Finally, in mammals, the scaling of stride frequency and V with body size is matched by a similar scaling exponent for V_{max}. Hence mammalian muscles operate at the same V/V_{max} values. Supported by NIH AR38404.

13.5

OXYGEN CONSUMPTION CORRELATES WITH TRUNK MUSCLE METABOLIC ENZYME ACTIVITIES IN LARVAL AND EARLY JUVENILE CALIFORNIA HALIBUT, PARALICHTHYS CALIFORNICUS.
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The activity of the mitochondrial enzyme citrate synthase and the glycolytic enzyme lactate dehydrogenase of the 'white' (fast-twitch, glycolytic) trunk muscles of halibut correlated with resting (i.e. maintenance, post-absorptive) and routine (maximum specific dynamic action, post-prandial) rates of oxygen consumption, respectively. The difference between these rates of oxygen consumption represent a kind of scope for metabolism. The relative concentration of the two enzymes represent an index of the metabolic 'poise' of the muscle, that is, its aerobic and anaerobic metabolic capacity. This can be thought of as a tissue level index of metabolic scope. The 'white' trunk musculature is the largest organ system of most fish (>50% of body mass), known to be used for high speed swimming and used as an energy depot. It is speculated that the fish's growth metabolism has produced similar trends in both whole-fish and white trunk muscle measurements of metabolic scope.

13.6

SKELETAL MUSCLE GLUCONEOGENESIS: GLYCOGEN SYNTHESIS FROM LACTATE IS STIMULATED BY EPINEPHRINE.
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Reptilian skeletal muscle is known to possess a considerable gluconeogenic capacity in vitro. It is known that this mechanism is responsible for at least 2/3 the glycogen replenishment following exhaustive exercise in vivo, a period when plasma catecholamines are elevated. Experiments were conducted to determine what influence post-exercise epinephrine (E) levels have on muscle glycogenesis, since E is understood to depress hepatic glycogen synthesis in other vertebrates. Red and white fiber bundles from the iliofibularis (rIF, wIF) muscle of the lizard *Dipsosaurus dorsalis* were incubated 2 hr at 40°C, pH = 7.2 in the presence or absence of 15 ng/ml E and 15 mM lactate, 8.5 mM glucose, or lactate plus glucose; conditions similar to those post-exercise. Labelled CO_2 evolution was used as evidence of substrate oxidation, while label incorporation into glycogen was used as evidence of glycogenesis. Lactate and glucose metabolism in rIF was always approximately 3X that in wIF. Approximately 4-5 times as much lactate carbon as glucose was oxidized or converted to glycogen in both rIF and wIF, independent of E. Epinephrine stimulated lactate metabolism, but had no effect on glucose metabolism. Epinephrine increased lactate incorporation into glycogen 2-3X, but stimulated lactate oxidation in wIF only. Total lactate metabolism (oxidation + glycogenesis) was stimulated by E in both rIF and wIF, in both the presence and absence of glucose. We conclude that the catecholamine changes associated with exercise in lizards facilitate muscle glycogen resynthesis and lactate removal by stimulating muscle gluconeogenesis. Supported by NSF DCB 8615603.