Integrating the Physiology, Mechanics and Behavior of Rapid Running Ghost Crabs: Slow and Steady Doesn't Always Win the Race
Author(s): Robert J. Full and Randi B. Weinstein

Integrating the Physiology, Mechanics and Behavior of Rapid Running Ghost Crabs: Slow and Steady Doesn't Always Win the Race[1]

Robert J. Full and Randi B. Weinstein

Department of Integrative Biology, University of California at Berkeley, Berkeley, California 94720

Synopsis. In 1979 Bliss predicted that, "land crabs are and will undoubtedly continue to be promising objects of scientific research." Studies of rapid running ghost crabs support her contention and have resulted in several general findings relating to locomotion and activity. 1) Energy exchange mechanisms during walking are general and not restricted to quadrupedal and bipedal morphologies. 2) "Equivalent gaits," such as trots and gallops, may exist in 4-, 6- and 8-legged animals that differ greatly in leg and skeletal (*i.e.,* exo- *vs.* endoskeletal) design. These findings support the hypothesis that terrestrial locomotion in many species can be modeled by an inverted pendulum or spring-mass system. 3) An open circulatory system and chitin-covered gills do not necessarily limit the rate at which oxygen consumption can be increased or the factorial increase in oxygen consumption over resting rates. 4) Interspecific and intraspecific (*i.e.,* ontogenetic) scaling of sub-maximal oxygen consumption and maximal aerobic speed can differ significantly. 5) Locomotion at speeds above the maximal aerobic speed requiring non-aerobic contributions may be far more costly than can be predicted from aerobic costs alone. The cost of transport may attain a minimum at less than maximum speed. 6) The speed which elicits maximal oxygen consumption during continuous exercise is attained at moderate walking speeds in crabs and probably other ectotherms. Speeds 15- to 20-fold faster are possible, but cannot be sustained. 7) The low endurance associated with the low maximal oxygen consumption and maximal aerobic speed of ectotherms moving continuously can be increased or decreased by altering locomotor behavior and moving intermittently. Ectotherms can locomote at high speeds and travel for considerable distances or remain active for long periods by including rest pauses. Alternatively, intense activity with extended exercise periods or with short pause periods may actually reduce behavioral capacity or work accomplished relative to continuous activity during which the behavior is carried out at a lower intensity level without pauses.

INTRODUCTION

In 1979 Bliss outlined the morphological, physiological and behavioral "solutions" to the problems of terrestrial life in crabs. In particular, she documented the importance of activity and locomotion in dealing with predators, dehydration and reproduction.

Crabs engage in daily or seasonal journeys to spawn (Cargo, 1958; Saigusa, 1981; Wilber and Herrnkind, 1986), to reduce physiological stresses such as temperature and salinity fluctuations and mechanical disturbance (Edwards, 1958; Wilber and Herrnkind, 1986), and to feed (Rangeley and Thomas, 1987). Crab movements can be grouped into three general categories (Hill, 1978); 1) long distance migration, often a prelude to reproduction in the sea, 2) free-ranging movements, such as those involved in foraging activity, and 3) restricted move-

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ments near the home site, including construction and defense of burrows.

During long distance migrations, mature female blue crabs may travel as far as 1,000 m per day to reach spawning areas (Cargo, 1958). Christmas crabs, *Gecarcoidea natalis,* travel hundreds of meters to mate and release larvae during their annual terrestrial migration (Hicks, 1985). Short-distance journeys away from the burrow or home site provide crabs with access to food and the opportunity to investigate the local area while remaining within safe distance of a refuge. Sand crabs, *Scopimera inflata,* deposit feed as they repeatedly move short distances (0.5 m) to and from their burrow (Fielder, 1970). Soldier crabs, *Mictyris longicarpus,* forage for about 1 to 2 hr during a single tidal cycle, alternating periods of walking and feeding. After feeding, armies of soldier crabs wander over distances in excess of 400 m at average speeds of 0.15 m sec^{-1} before returning to their home site (Cameron, 1966).

In addition to low intensity activity, several species of crab are also capable of rapid responses to escape from predators, capture prey, and defend territories. Land crabs can run from birds, larger crabs and other species that act as predators (Cameron, 1966; Hughes, 1966; Knopf, 1966; Wolcott, 1978; Beever et al., 1979; Trott, 1988). Other crabs are effective at catching fast moving prey (Hughes, 1966). Since territoriality is common in ocypodids (*e.g., Uca* and *Ocypode*), intense activity can occur during burrow defense (Dunham and Gilchrist, 1988). When an intruder tries to enter another crab's burrow, the result can be an aggressive interaction that can involve rapid movements or lead to the use of force.

Among crabs in general, ghost crabs in the genus *Ocypode* have been particularly valuable experimental animals for studies of locomotion and typify the Krogh Principle, "For many problems there is an animal on which it can be most conveniently studied." Ghost crabs can search for prey on open beaches and forage as far as 300 m a night (Wolcott, 1978). They also possess the capacity for high intensity activity. A resident at the mouth of a burrow often responds to an intruder by "pouncing"

(Evans et al., 1976). The ghost crab, *Ocypode,* is the fastest crustacean observed to date, moving at speeds in excess of 3 m sec^{-1} on hard surfaces (Hafeman and Hubbard, 1969; Burrows and Hoyle, 1973). As the French naturalist Bosc noted in 1802, "when they fear some danger, they save themselves by walking sideways into their burrow with such rapidity that this naturalist was a long time observing them before forming an idea about the species of animal which was fleeing before him; it finally took a horse to procure several specimens of them, again after several futile attempts. One knows well than an animal so difficult to catch cannot serve commonly as nourishment; thus in Carolina no one makes any use of them" (quoted in Milne and Milne, 1946). Ghost crab locomotion has been examined to test hypotheses in neurobiology, biomechanics, and exercise physiology.

Because of their locomotor capacity, the study of eight-legged, sideways movement has proved to be important in the search for general principles amidst the spectacular diversity in locomotor morphology, physiology and behavior. The results of many of these studies have been reviewed by Herreid and Full (1988) in *The Biology of Land Crabs* (Burggren and McMahon, 1988). In the discussion that follows, we will integrate data from various areas in an attempt to provide a more *complete* picture of crab and animal locomotion. In doing so, we will highlight the general principles of locomotion that have arisen from studies on ghost crabs (*Ocypode quadrata*), discuss predictions from laboratory studies as they pertain to ghost crab locomotion in every day life and, finally, suggest areas for future study.

For the most part, laboratory studies on ghost crabs and most other animals have elucidated the relationships between morphology, physiology and performance during steady-state, continuous locomotion. We will summarize these advances, but emphasize the transition from continuous activity to intermittent and high speed locomotion. Recent research on ghost crab exercise has revealed that this transition is an important factor in assessing the limits of performance. Studies of intermittent locomotion, in particular, have demonstrated the essen-

tial role of behavior and have even led to a challenge of Aesop's fable, *The Hare and Tortoise* (1947).

HOW DO CRABS MOVE?—MECHANICS

Walking

At speeds less than 0.4 m sec^{-1}, 30 g ghost crabs walk (Blickhan and Full, 1987). Walking crabs use an alternating tetrapod gait (Barnes, 1975; Clarac, 1981). Legs 2–5 are coordinated so that two sets of walking legs alternate, R2 L3 R4 L5 with L2 R3 L4 R5 (R = right side; L = left side). Each set of legs functions as an inverted pendulum over which the crab vaults. Potential energy of the body or center of mass fluctuates out of phase with forward kinetic energy. Vaulting over stiffened legs conserves mechanical energy that would otherwise be generated by muscles. The maximum energy exchange in ghost crabs of 55% at 0.2 m sec^{-1} is similar to that found in birds and mammals (Fig. 1A; Cavagna *et al.*, 1977; Heglund *et al.*, 1982). Pendulum-like exchange between kinetic and potential energy appears to be a very general mechanism that is not restricted to a particular skeletal type (exoskeleton *vs.* endoskeleton), number of legs, or leg position relative to the body (sprawled *vs.* upright).

Trotting

At speeds greater than 0.4 m sec^{-1}, ghost crabs trot or run slowly (Blickhan and Full, 1987). Energy recovery from pendulum-like exchange is reduced (Fig. 1A), despite the fact that the stepping pattern is not altered. In a trot, fluctuations of the body's potential and kinetic energy shift from being out of phase, as in the walking gait, to being largely in phase. The synchronous oscillation of the body's potential and kinetic energy is analogous to a bouncing ball or pogo stick. Stride frequency increases linearly with speed as seen in trotting quadrupedal mammals (Fig. 1B; Heglund *et al.*, 1974). Moreover, the time course and relative magnitude of ground reaction forces are remarkably similar to those found in trotting quadrupedal mammals (Cavagna *et al.*, 1977; Heglund *et al.*, 1982; Blickhan and Full, 1987). Ghost crabs clearly use a running or bouncing gait

similar to a trot, the only difference being the lack of an aerial phase. The absence of an aerial phase does not appear sufficient to exclude a gait from being considered a run (McMahon, 1985; McMahon *et al.*, 1987). Since gait changes in ghost crabs can occur without any obvious change in stepping pattern and a running gait may not require an aerial phase, gaits may be best defined by a more complete quantification of locomotor dynamics (*i.e.,* kinetics and kinematics).

Galloping

Ghost crabs are capable of high speeds (*i.e.,* 3–4 m sec^{-1}; Hafeman and Hubbard, 1969; Burrows and Hoyle, 1973). As their generic name (*Ocypode*—swift of foot) suggests, they are among the fastest terrestrial invertebrates. At speeds greater than 0.8–0.9 m sec^{-1}, ghost crabs run fast or gallop (Blickhan and Full, 1987). Fluctuations of the body's potential and kinetic energy remain in phase (Fig. 1A). The stepping pattern becomes altered, muscle electrical activity is changed and leg five and sometimes four are held off the ground and do not participate in locomotion (Burrows and Hoyle, 1973). Stride frequency becomes independent of speed (Fig. 1B). Faster speeds are attained by leaping and taking longer strides. Aerial phases appear. Strain (*i.e.,* deformation under stress) in the exoskeleton of legs changes significantly at the trot-gallop transition as it does in bones of horses, dogs and goats (Biewener and Taylor, 1986). Although mammals and crabs alter musculo-skeletal function at this transition speed, differences in skeletal design are apparent since relative peak strain in the crab exoskeleton increases over that observed in a walk or trot in contrast to galloping mammals in which endoskeletal strain decreases (Fig. 1C; Full *et al.*, 1991).

Studies on ghost crab locomotion have suggested the possibility that "equivalent gaits" exist in species that differ greatly in morphology and physiology. The change in gait from a trot to a gallop occurs at almost the identical speed and stride frequency predicted for the trot-gallop transition of a quadrupedal mammal of the same mass (Heglund *et al.*, 1974; Heglund and Taylor, 1988;
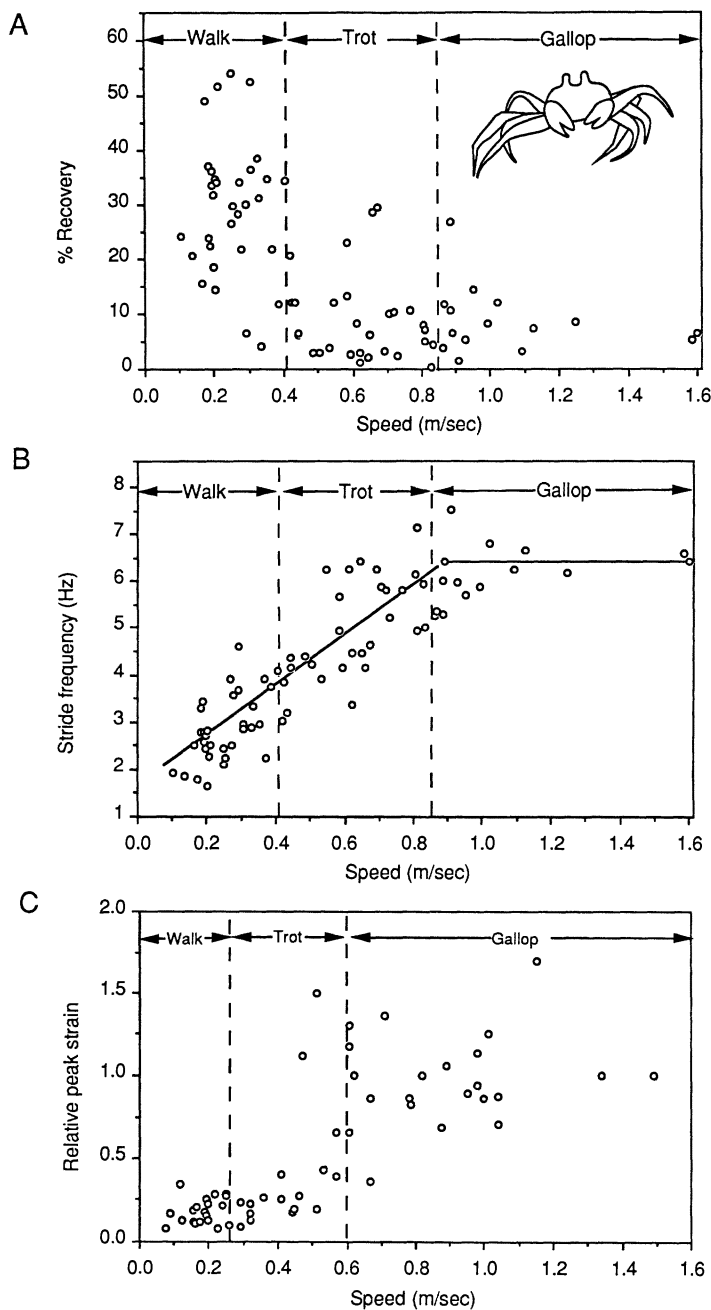
FIG. 1. Biomechanics of ghost crab locomotion. A. Energy recovery as a function of speed in 27 g crabs (Blickhan and Full, 1987). A value of 100% would indicate complete transfer between kinetic and gravitational potential energy, as in a ideal pendulum. Ghost crabs recover the maximum amount of energy (55%) at 0.2 m sec^{-1}. B. Stride frequency as a function of speed in 27 g crabs. The transition from a trot to a gallop occurs at nearly the same speed and frequency as the trot-gallop transition in quadrupeds. C. Peak strain in the exoskeleton as a function of speed in 14 g crabs. During a gallop, the relative peak strain of the meropodite of the second "walking" leg increases significantly over that observed in a walk or trot. Note that the walk-trot and trot-gallop transitions occur at slower speeds in 14 g crabs compared to medium-sized, 27 g, crabs (Full *et al.*, 1991).

Full, 1989). These studies have led to further research on six-legged locomotors, insects. Research on the mechanics of cockroaches has shown that 2-, 4-, 6- and 8-legged animals can generate comparable ground reaction force patterns (Full and Tu, 1990, 1991). Despite the obvious diversity, all can run or bounce in a similar manner. A mass on top of a spring appears to be an appropriate starting point for a model of terrestrial locomotion (McMahon, 1985; Blickhan, 1990; McMahon and Cheng, 1990).

WHAT POWERS LOCOMOTION? — ENERGETICS

Aerobic metabolism

Ghost crabs increase oxygen uptake rapidly at the onset of exercise (Full and Herreid, 1983; Full, 1987). The time required to attain 50% of the steady state oxygen consumption (*i.e.,* 30–60 sec) is within the range observed for mammals and insects (Full, 1987). This suggests that reliance on chitin-covered gills and an open circulatory system does not necessarily restrict a rapid aerobic response, despite the fact that other exercising crabs show far more sluggish aerobic kinetics (Wood and Randall, 1981a; Herreid *et al.,* 1983; Full and Herreid, 1984; Full *et al.,* 1985). Below speeds that elicit maximal rates of oxygen consumption (*i.e.,* less than 0.2 m sec^{-1}), the energy required by ghost crabs for sustained, constant speed locomotion is supplied by aerobic ATP production (Fig. 2A). Steady-state oxygen consumption increases linearly with speed in ghost crabs as is typical for most pedestrians.

Anaerobic metabolism

Accelerated glycolysis in ghost crabs contributes little to energy production during steady-state, submaximal exercise, even at speeds that elicit 70–90% of the maximal oxygen consumption (Full, 1987). As in other species, rapid glycolysis does occur at the onset of submaximal exercise (*i.e.,* the first 5–10 min). Surprisingly, lactate removal in ghost crabs can actually exceed production during exercise and can result in a decrease in whole body lactate after 10–15 min. Other crab species show a far greater

reliance on anaerobic metabolism even during submaximal exercise (Burke, 1979; Wood and Randall, 1981b; Full and Herreid, 1984). Whole body lactate continues to increase in fiddler crabs throughout a 15 min exercise bout and is associated with a very slow increase in oxygen uptake (Full and Herreid, 1984).

At speeds greater than the speed that elicits the maximal rate of oxygen consumption (*i.e.,* maximum aerobic speed or greater than 0.2 m sec^{-1} for a medium-sized ghost crab at 24°C), ghost crabs rely primarily on non-aerobic energy sources (Fig. 2A). Crabs exercising at the walk-trot transition (*i.e.,* 0.4 m sec^{-1}) show large increases in muscle lactate and a significant depletion of arginine phosphate (Full and Prestwich, 1986). The rate of lactate production and arginine phosphate depletion increases further during exercise at faster speeds that fall in the middle of the trotting gait (*i.e.,* 0.6 m sec^{-1}). The contribution of ATP from aerobic metabolism may actually decrease at these high speeds because the maximal rate of consumption is not attained before fatigue. Conservative estimates of the total cost of locomotion at mid-trot speed reveal an 35-fold increase above resting rates (Fig. 2A). By contrast, extrapolation of the aerobic cost to mid-trot speed shows only a 17-fold increase. Locomotion at speeds greater than the maximal aerobic speed can be far more costly than can be predicted from aerobic costs. The total energy utilization rate may increase curvilinearly as speed is increased.

Minimum cost of locomotion

At speeds less than the maximal aerobic speed, the energetic cost of travelling a given distance (*i.e.,* the cost of transport) decreases and approaches a minimum (Fig. 2B). By the standard comparison of the minimum cost of transport (*i.e.,* the slope of the steady-state oxygen consumption *vs.* speed function; Taylor *et al.,* 1970), ghost crabs fall within the 95% confidence limits for all pedestrians of the same body mass (Full, 1987). Despite running sideways with eight armored legs, cost is similar to 2-, 4-, 6-, 8-, 40- and even 100-legged travelers (Full, 1989; Full *et al.,* 1990).

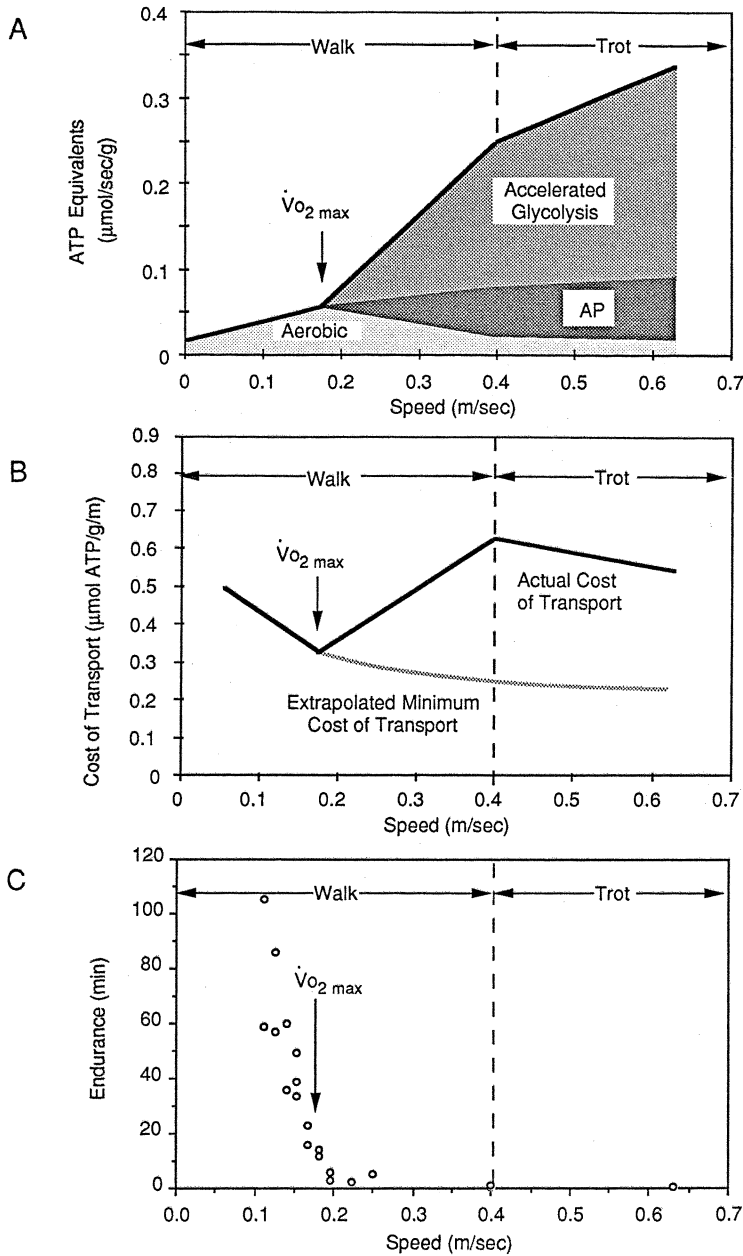The minimum cost of transport evalua-

FIG. 2. Locomotion energetics of the ghost crab. A. Aerobic, high energy phosphate, and glycolytic contributions in walking and trotting crabs (27 g; Full and Prestwich, 1986). The total number of ATP equivalents increases non-linearly at speeds above that which elicit maximal oxygen consumption. B. Total cost of locomotion as a function of speed for 27 g crabs. The total cost of transport includes estimates of glycolytic and high-energy phosphate contributions. The total cost of transport is minimal at the maximum aerobic speed. C. Endurance or time to fatigue as a function of speed for 27 g crabs. Endurance decreases exponentially above the speed which elicits maximal oxygen consumption, the maximum aerobic speed (Full, 1987).

tion is typically restricted to aerobically supported speed ranges (Taylor *et al.*, 1970; Heglund *et al.*, 1982). This speed range is narrow for ghost crabs and most other ectotherms relative to endotherms. If total cost per distance is considered for ghost crabs, then a minimum appears to be attained in the middle of the walking gait where exoskeletal strain is low, maximum mechanical energy exchange occurs, maximum oxygen consumption is attained, and non-aerobic sources are not heavily depended upon. Total cost of transport is minimized at midwalking speed because of the curvilinear function of total cost and speed, which is similar to the function observed in swimming fish.

Effect of growth and body mass

The large size range of ghost crabs (*i.e.*, 2–70 g) provides a unique opportunity to test whether intraspecific scaling of aerobic cost follows the trends observed for interspecific variation. Mass-specific resting and maximal oxygen consumption decrease with body mass intraspecifically, as observed interspecifically (Fig. 3A). When crabs grow, their mass-specific minimum cost of transport (*i.e.*, slope of the mass-specific, steadystate oxygen consumption *vs.* speed function) decreases and follows the interspecific relationship which predicts the cost of over 150 pedestrian species (Full, 1989). The y-intercept of the mass-specific, steady-state oxygen consumption *vs.* speed function does not scale as predicted. At slow walking speeds, large crabs (71 g) consume as much oxygen per unit mass as crabs less than one half their mass (Full, 1987). The higher than predicted aerobic cost of exercise in large crabs is significant, not only because of the consequences of the greater cost, but perhaps more importantly because the elevated cost affects endurance. As has been shown in lunged and lungless salamanders, aerobic cost and maximal oxygen consumption interact to determine the speed at which maximal oxygen consumption is attained (Full *et al.*, 1988). High aerobic costs of locomotion result in maximal oxygen consumption rates being attained at relatively low speeds and lead to an increased reliance on anaerobic metabolism.

Effect of temperature

Ghost crabs acclimated at 24°C reach thermal equilibrium with the environment at ambient temperatures (T_{amb}) of 15 and 24°C. Steady-state oxygen consumption decreases significantly from 24 to 15°C (Fig. 3B). The decrease is due to lower resting rates of oxygen uptake and a lower y-intercept of the steady-state oxygen consumption *vs.* speed function. The minimum cost of transport (*i.e.*, the slope of the steadystate, oxygen consumption *vs.* speed function) does not change. The independence of the minimum cost of transport with changes in temperature has been shown in both vertebrates (John-Alder and Bennett, 1981; Rome, 1982) and arthropods (Herreid *et al.*, 1981; Full and Tullis, 1990). At T_{amb} of 30°C and a low relative humidity, body temperatures of ghost crabs are only 24°C (Weinstein and Full, 1990*b*), indicating the capacity to maintain body temperature by evaporative cooling. Steady-state oxygen consumption at an ambient temperature of 30°C only increases 1.8-fold at faster speeds, despite the fact that the ghost crab's body temperature is the same as at an ambient temperature of 24°C where oxygen consumption increases 6.5-fold. Dehydration, as well as temperature, may have substantial effects on gas transport. Relatively slow speeds may require anaerobic metabolism due to the dehydration.

HOW LONG CAN LOCOMOTION BE SUSTAINED?—ENDURANCE

Maximal oxygen consumption

At speeds eliciting oxygen consumption rates that are maximal, endurance of the ghost crab declines and locomotion is considered unsustainable (Fig. 2C). All else being equal, animals with greater aerobic capacities will be able to sustain higher speeds. Ghost crabs can attain maximal rates of oxygen consumption that are similar to those measured in other ectotherms, such as lizards (Bennett, 1982). Using chitin-covered gills and an open circulatory system does not necessarily restrict the capacity for oxygen uptake. Ghost crabs can increase oxygen consumption as much as 12-fold over resting rates (Full and Herreid, 1983),
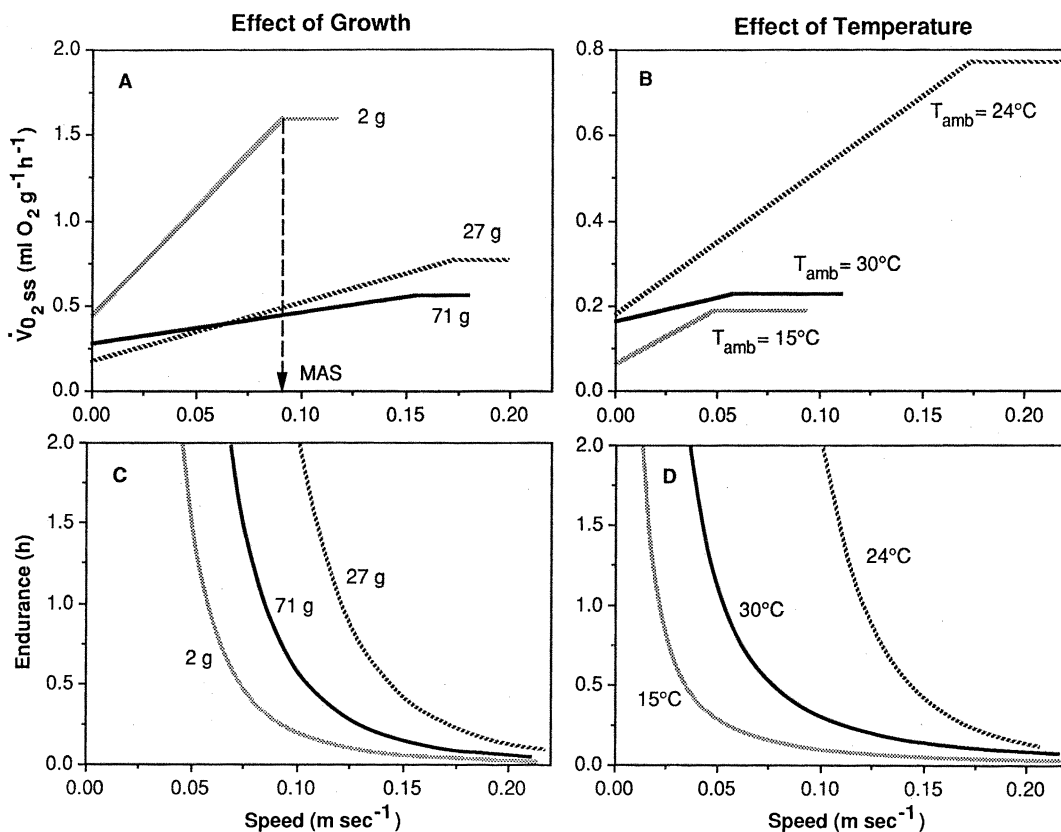
FIG. 3. Effect of growth and temperature on the locomotion energetics of ghost crabs. A. Steady-state oxygen consumption as a function of speed for 2, 27, and 71 g crabs (Full, 1987). Maximum aerobic speed (*i.e.*, the speed which elicits maximal oxygen consumption, MAS) is the highest in 27 g crabs. The mass-specific minimum cost of transport (slope of line) decreases with an increase in body mass. B. Steady-state oxygen consumption as a function of speed and ambient temperature for 27 g crabs (Weinstein and Full, 1990*b*). Maximum aerobic speed and maximal oxygen consumption are greatest at an ambient temperature of 24°C. C. Endurance time as a function of speed for 2, 27, and 71 g crabs. Endurance capacity is correlated with maximum aerobic speed. Crabs of 27 g show the greatest endurance capacity. D. Endurance time as a function of speed and ambient temperature for 27 g crabs. Endurance capacity was correlated with maximum aerobic speed. Crabs show the greatest endurance at an ambient temperature of 24°C.

an aerobic factorial scope comparable to that of exercising lizards and mammals (*i.e.*, 5- to 15-fold; Bennett, 1982; Taylor *et al.*, 1980). In contrast to ghost crabs, most other crustaceans have a more modest capacity to increase oxygen consumption (*i.e.*, 2- to 6-fold; McMahon, 1981).

Maximal aerobic speed

Maximal aerobic speed (*i.e.*, the speed at which maximal oxygen consumption is attained; John-Alder and Bennett, 1981) is highly correlated with sustainable activity. When speed is increased and maximal rates of oxygen consumption are approached,

endurance declines (Fig. 2C). In ghost crabs speeds that are two or three times the maximal aerobic speed can only be maintained for 50 and 36 seconds, respectively (Full and Prestwich, 1986). Speeds 15 to 20 times the maximal aerobic speed are possible, but can only be maintained for a few seconds (Full and Prestwich, 1986).

Effect of growth and body mass

As ghost crabs grow, mass-specific maximal oxygen consumption decreases in parallel with resting oxygen uptake (Full, 1987). Intraspecific scaling of maximal oxygen consumption in ghost crabs follows a func-

tion similar to interspecific scaling in lizards (Bennett, 1982) and mammals (Taylor *et al.*, 1980).

Maximal rates of oxygen consumption alone are an insufficient predictor of sustainable activity (Full *et al.*, 1988). It is the interaction of the cost of locomotion and maximal oxygen consumption that determines the maximum aerobic speed. Small ghost crabs (≤ 2 g) have the highest rates of mass-specific maximal oxygen uptake, but also have the greatest mass-specific cost of locomotion (*i.e.*, submaximal oxygen consumption) relative to larger crabs (Fig. 3A). As a result, small ghost crabs attain maximal oxygen consumption at relatively low speeds (*i.e.*, they have a low maximal aerobic speed). Intermediate sized crabs (~ 27 g) have a mass-specific, maximal oxygen consumption and cost of locomotion that are greater than those of the largest crabs, but less than those of the smallest crabs. Large ghost crabs (≥ 71 g) have the lowest rates of mass-specific, maximal oxygen uptake and the lowest mass-specific cost of locomotion. However, the largest crabs do not have the greatest maximal aerobic speed as predicted from interspecific scaling. Because the mass-specific cost of locomotion in the largest crabs (*i.e.*, y-intercept) is somewhat greater than predicted from interspecific scaling relationships, the largest crabs attain maximal rates of oxygen consumption at speeds that are less than the intermediate sized animals, and have lower endurance (Fig. 3C). Intermediate sized crabs actually have the greatest maximal aerobic speed and the greatest endurance.

Effect of temperature

Locomotor endurance is highly dependent on ambient temperature in ectotherms (John-Alder and Bennett, 1981; Full and Tullis, 1990). In ghost crabs, decreases in maximal oxygen consumption and maximal aerobic speed at 15°C are correlated with a lower endurance than at 24°C (Fig. 3D). Resting metabolic rates are similar at an ambient temperature of 24 and 30°C, but maximal oxygen consumption, maximal aerobic speed, and consequently, endurance, are significantly reduced when ambient temperature is 30°C (Fig. 3D). Since body temperature is the same at 24 and 30°C,

dehydration may have adverse effects on stamina. The endurance of constant speed exercise is greatest when ambient temperature is 24°C.

How Does Physiology Affect Locomotor Behavior?—Intermittent Activity

For ghost crabs living on exposed sandy beaches, the burrow provides safety from extreme environmental fluctuations, predators, and competitors (Lighter, 1974). When the ghost crab, *Ocypode ceratophthalmus*, emerges from its burrow, it makes several short trips within a few meters of the burrow before venturing over greater distances (Hughes, 1966). In *Ocypode kuhlii*, these short forays last an average of 90 sec (Evans *et al.*, 1976). Several species of ghost crab actively search for live prey (*e.g.*, small crustaceans, including juvenile *Ocypode*, and mollusks; Hughes, 1966; Wolcott, 1978; Trott, 1988). Long distance foraging in *Ocypode quadrata* generally occurs within several hundred meters of the burrow (Wolcott, 1978). Even during the longest journeys, ghost crabs appear to make frequent starts and stops. As do most animals, they move intermittently. Yet, as we have already discussed, many proposed limitations of terrestrial locomotion are based on steady-state, continuous activity. Results from studies on steady-state exercise have been used 1) to propose design constraints for oxygen transport (Weibel and Taylor, 1981), 2) to advance hypotheses concerning the evolution of endothermy (Bennett and Ruben, 1979) and 3) to predict natural locomotory behavior (Bennett *et al.*, 1984; Hertz *et al.*, 1988). These and other proposed performance or design constraints based solely on steady-state locomotion may require revision when results are obtained from intermittent exercise. Alternating periods of high-intensity exercise with pause periods, during which low-intensity or no work is done, can alter metabolic responses and endurance (see review by Saltin *et al.*, 1976).

Endurance and distance capacity

Ghost crabs fatigue after 41 min of continuous walking at 0.15 m sec^{-1}, a total distance of 372 m (Weinstein and Full, 1990*a*,
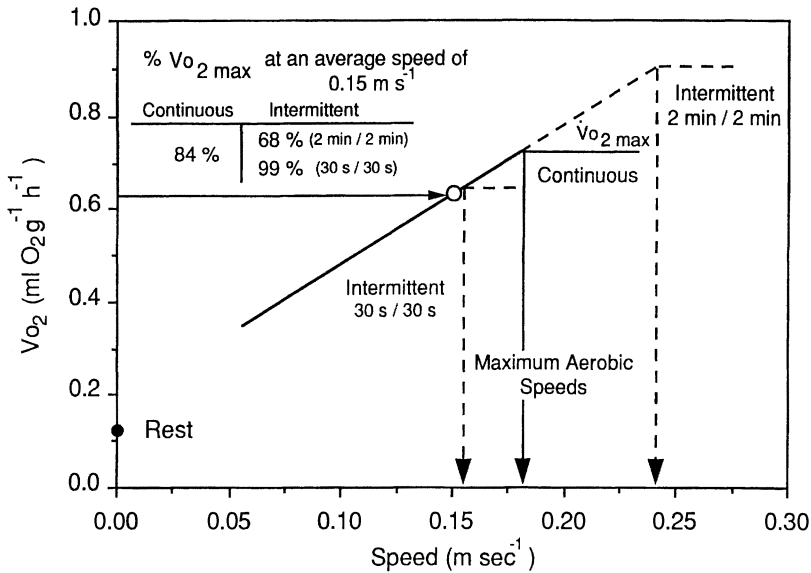
FIG. 4.   Effect of intermittent locomotion on relative workload in ghost crabs. Steady-state oxygen consumption of continuous locomotion increases linearly with speed (solid line) for 27 g crabs until it attains a maximum rate ($\dot{V}O_2$max) at the maximum aerobic speed. Continuous locomotion at 0.15 m sec^{-1} requires 84% $\dot{V}O_2$max. Crabs increase their effective $\dot{V}O_2$max and maximum aerobic speed (right most dashed line) by exercising intermittently using 2 min exercise and pause periods. A submaximal workload of 0.15 m sec^{-1} becomes a smaller fraction (68%) of the effective maximal rate of oxygen consumption during intermittent exercise. Intermittent exercise at an average speed of 0.15 m sec^{-1} using 30 sec exercise and pause periods decreases the effective $\dot{V}O_2$max and maximum aerobic speed (left most dashed line). The workload at these shorter intervals is equivalent to 99% $\dot{V}O_2$max.

1992; Table 1). A speed of 0.15 m sec^{-1} is below the speed at which maximal oxygen consumption is attained. Crabs exercising at 0.30 m sec^{-1}, a speed above the maximal aerobic speed, can only sustain this speed for 7.5 min, a distance of 135 m. If locomotion is done intermittently by alternating 2 min bouts of exercise at 0.30 m sec^{-1} with 2 min pauses, then crabs fatigue after 87 min, a total distance of 787 m. Using this protocol, crabs can exercise at a speed (0.30 m sec^{-1}) above the maximal aerobic speed repeatedly as long as pauses are included. Distance capacity (*i.e.*, distance traveled to fatigue) increases by 5.8-fold compared to continuous exercise at this speed, and by 2.1-fold compared to continuous exercise at the same average speed (0.15 m sec^{-1}). Exercise periods of 3, 4, and 5 min (exercise/pause duration = 1) decrease distance capacity relative to continuous exercise at the same average speed. When shorter pause periods (0.5 and 1 min) are alternated with 2 min exercise periods, distance capacity also decreases.

"Altering" the maximal aerobic speed

Relative to continuous locomotion, distance capacity can be increased or decreased by moving intermittently (Weinstein and Full, 1992; Table 1). Particular exercise and pause periods can increase the effective maximum aerobic speed of a ghost crab (Fig. 4). Crabs can travel the same distance in a given time period without fatiguing by moving rapidly at speeds above that which elicits maximal oxygen consumption as long as pauses are included. Intermittent locomotion can decrease the relative work load at a given speed. A speed that requires 84% of maximal oxygen consumption during continuous walking may only demand 68% of the effective maximal oxygen consumption if a crab walks twice as fast, but rests half the time (2 min exercise, 2 min pause). These results suggest that the limitations associated with low maximal oxygen consumption and maximal aerobic speed of ectotherms (*i.e.*, relative to endotherms) can be reduced by simply adopting a different locomotor behavior. In addition to the

Table 1. *Distance capacity during intermittent exercise.*

Exercise duration (sec)	Pause duration (sec)	Total distance travelled before fatigue (m)		
		Intermittent exercise	Continuous exercise at same AvS	Continuous exercise at same AbS
30	30	105.3 ± 20.8[a]	371.6 ± 42.6	134.7 ± 17.2
120	120	786.7 ± 142.6[a,b]	371.6 ± 42.6	134.7 ± 17.2
360	360	268.2 ± 77.8[b]	371.6 ± 42.6	134.7 ± 17.2
480	480	201.9 ± 54.0[a,b]	371.6 ± 42.6	134.7 ± 17.2
600	600	197.5 ± 47.5[a,b]	371.6 ± 42.6	134.7 ± 17.2

Distance capacity for intermittent exercise and continuous exercise are given as mean ± SE (Weinstein and Full, 1992). The absolute speed (AbS) for each intermittent protocol is 0.30 m sec^{-1} (n = 5). n = 11 for continuous exercise at the same AbS. Distance capacity for continuous exercise at the same average speed (AvS; 0.15 m sec^{-1}) is recalculated from data reported by Full (1987) over the range of speeds from 0.13–0.19 m sec^{-1}.
[a] Significantly different from the distance capacity at the same AvS ($P < 0.05$).
[b] Significantly different from the distance capacity at the same AbS ($P < 0.05$).

advantages in distance capacity, intermittent behavior allows time for sensing the environment or performing other less strenuous behaviors during the pauses.

Other combinations of exercise and pause intervals can decrease distance capacity relative to locomotion at the same average speed (Weinstein and Full, 1992; Table 1). Crabs can fatigue sooner in a given time period by moving rapidly at speeds above that which elicits maximal oxygen consumption. Intermittent locomotion can increase the relative work load at a given speed. A speed that requires 84% of maximal oxygen consumption during continuous walking may demand 99% of the effective maximal oxygen consumption if a crab walks twice as fast, but rests half the time (30 sec exercise, 30 sec pause; Fig. 4). Behavioral capacity or work done during intense activity with extended exercise periods or with short pause periods may be less than if that behavior were carried out at a lower intensity level without pauses.

Metabolic response

Intermittent activity differs from continuous activity in that the former relies primarily on the rate at which systems turn on and off during transitions to or from a steady-state. At the onset of exercise before oxygen uptake has attained a steady-state, the concentration of lactic acid can increase due to accelerated glycolysis and high-energy phosphate and oxygen stores can be depleted. During recovery or a pause from activity, lactate can be cleared and high-energy phosphate and oxygen stores can be replenished. Measurements of muscle
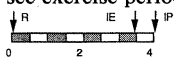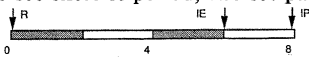
metabolites in ghost crabs taken at the end of exercise and pause intervals suggest that 120 sec pause periods are adequate for some lactate clearance and phosphagen repletion, but 30 sec pause periods are insufficient (Weinstein and Full, 1990a; Table 2). Differences in distance capacity found for intermittent *vs.* continuous exercise, even at the same average speed, are most likely associated with the kinetics of fatigue-producing agents relative to the rate of recovery processes. The dynamics of physiological rate processes can significantly affect the duration of locomotor behavior.

An apparent disadvantage of intermittent exercise is the high cost compared to continuous exercise. When calculated from the average rate of oxygen consumption during complete exercise-pause cycles, intermittent exercise is the same as or more expensive than continuous exercise both per time and per distance (Weinstein and Full, 1992). The difference in cost is most likely a consequence of the elevated metabolic rate during the pause periods, compared to the resting metabolic rate, and the high energy demand of the supramaximal speeds employed during the exercise periods (Full and Prestwich, 1986; Fig. 2B).

SUMMARY AND CONCLUSIONS

In 1979 Bliss predicted that, "land crabs are and will undoubtedly continue to be promising objects of scientific research." Studies of ghost crabs support her contention and have resulted in several general findings relating to locomotion and activity. By selecting ghost crabs to address general questions concerning locomotion, an inter-

TABLE 2. *Muscle metabolite concentration.*

Metabolite	Rest	Intermittent exercise group	Intermittent pause group
A. 30 sec exercise period; 30 sec pause period			
Lactate	2.2 ± 0.7	$*7.1 \pm 1.1$	$*9.9 \pm 1.0$
Arginine phosphate	21.5 ± 1.2	$*6.7 \pm 1.2$	$*7.7 \pm 1.2$
B. 120 sec exercise period; 120 sec pause period			
Lactate	1.2 ± 0.1	$*12.7 \pm 1.2$	$\dagger*9.4 \pm 1.4$
Arginine phosphate	21.3 ± 0.9	$*2.6 \pm 0.7$	$\dagger*8.3 \pm 1.7$

Means $\pm$ SE are reported for resting and exercising crabs. Values are expressed in μmol g^{-1} leg. In the experimental protocol, shaded bars represent exercise at 0.3 m sec^{-1} and white bars represent pause periods. Time is given in minutes. Arrows indicate when muscle samples were taken. Samples are labeled R (rest), IE (intermittent exercise), or IP (intermittent pause).
 * Significantly different from resting levels.
 † Intermittent pause levels are significantly different from intermittent exercise levels.

esting picture of the animal itself has emerged. Biomechanical studies show that in 30 g crabs the maximum energy exchange during walking occurs at the very slow speed of 0.2 m sec^{-1}. This speed may require the minimum amount of metabolic energy to travel a given distance when non-aerobic costs are considered. Maximal oxygen consumption is also attained at 0.2 m sec^{-1}. Above this speed, endurance during continuous locomotion is greatly reduced. Laboratory speed measurements of freely moving ghost crabs suggest that they do most often select the speed of 0.2 m sec^{-1} (Fig. 5).

High speed locomotion above 0.2 m sec^{-1} is not only possible, but may occur frequently in one of the fastest terrestrial arthropods (40% of the time; Fig. 5). Although high-speed locomotion is costly and could result in a greater risk of injury (*i.e.,* as shown by increased exoskeletal strains), it may not necessarily limit activity with respect to distance capacity if the activity is done intermittently. Ghost crabs and other ectotherms may obviate the limitation of a low maximal rate of oxygen consumption behaviorally by selecting a strategy that includes intermittent locomotion. Distance capacity can be increased by moving intermittently, but only if the exercise to pause ratios are within well defined limits set by the dynamics of physiological rate processes. In other words, the hare in Aesop's Fable (1947) could have beaten the tortoise easily using intermittent activity if it had only selected a shorter pause duration. The "rabbit of crustaceans" (Cott, 1930), ghost crabs, have shown us that slow and steady is not the only option.

Future studies on ghost crab locomotion, as well as on other species, should be directed toward at least two areas. First, additional performance criteria must be used to evaluate locomotor capacity. Many studies have determined the energetics and endurance of locomotion, but few have examined stability, maneuverability and durability. Likewise, the effect of variation in substrata (*e.g.,* sand *vs.* clay or hard rock; smooth *vs.* irregular terrain) has not been addressed adequately. Second, detailed field studies on
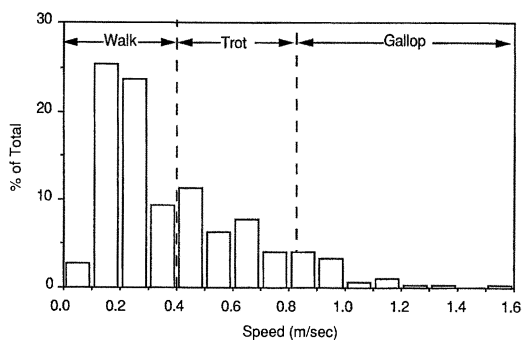
FIG. 5. Preferred speed of free locomotion by ghost crabs obtained on a track. 500 trials were recorded (Blickhan and Full, 1987). The preferred speed distribution showed a maximum at 0.1–0.3 m sec^{-1}, but speeds above the maximal aerobic speeds were frequent.

locomotion (*i.e.,* speed, frequency and duration of movement) must be conducted. Integration of physiology, mechanics and behavior requires knowledge of ecologically relevant capacities and the extent to which animals use these capacities in nature (Hertz et al., 1988).

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