

# Intermittent locomotor behaviour alters total work

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## 1. Introduction

The limits within which behaviour operates can be defined best by integrating biomechanics with physiology. In particular, the mechanistic bases for locomotion allow predictions about the work capacity available for migration, mating, foraging and fleeing. In this chapter, we use the terrestrial locomotion of ghost crabs as an example. The wealth of biomechanical and physiological laboratory data allows for testable predictions of field behaviour involving locomotion. First, we make predictions from biomechanics and energetics based on laboratory studies of steady-state locomotor behaviour. Second, we provide predictions based on laboratory studies of non-steady-state locomotor behaviour. Non-steady-state locomotor behaviour includes intermittent locomotion consisting of repeated bouts of exercise interspersed with pause periods. Third, we test laboratory-based predictions from biomechanics and energetics by reporting measured locomotor behaviour in the field. Data reveal that the total amount of work performed during a behavior depends on the rate of work, the duration of work and the extent to which the work is conducted intermittently. Finally, we examine the generality of the consequences of intermittent locomotor behaviour on total work. We compare species with diverse metabolic responses to locomotion.

## 2. Predictions from biomechanics and energetics based on laboratory studies of steady-state locomotor behaviour

Laboratory studies of ghost crabs (*Ocypode quadrata*) have examined the relationships between morphology, physiology and performance during steady-state, continuous locomotion. Studies of the biomechanics (Blickhan and Full, 1987), energetics and endurance (Full, 1987) of continuous locomotion by ghost crabs have proved to be important in the search for general principles of locomotion (see reviews by Full and Weinstein (1992) and Herreid and Full (1988)).

### 2.1 Biomechanics

The steady-state biomechanics and kinematics of terrestrial locomotion by ghost crabs have been characterized on miniature force platforms and motorized treadmills. At slow speeds, less than  $0.4 \text{ m s}^{-1}$ , 30 g ghost crabs use a walking gait (Blickhan and Full, 1987). In a walking gait, the potential energy of the center of mass is out of phase with its kinetic energy and is analogous to an inverted pendulum. The maximum energy exchange (transfer between kinetic and potential energy) is achieved at  $0.2 \text{ m s}^{-1}$ , a slow walking speed (*Figure 1(a)*). At speeds greater than  $0.4 \text{ m s}^{-1}$ , ghost crabs trot or run slowly (Blickhan and Full, 1987). In a trot, the potential and kinetic energy of the center of mass are in phase and the energy recovery from pendulum-like exchange is reduced. To maximize energy exchange, ghost crabs should move continuously at a speed of approximately  $0.2 \text{ m s}^{-1}$ .

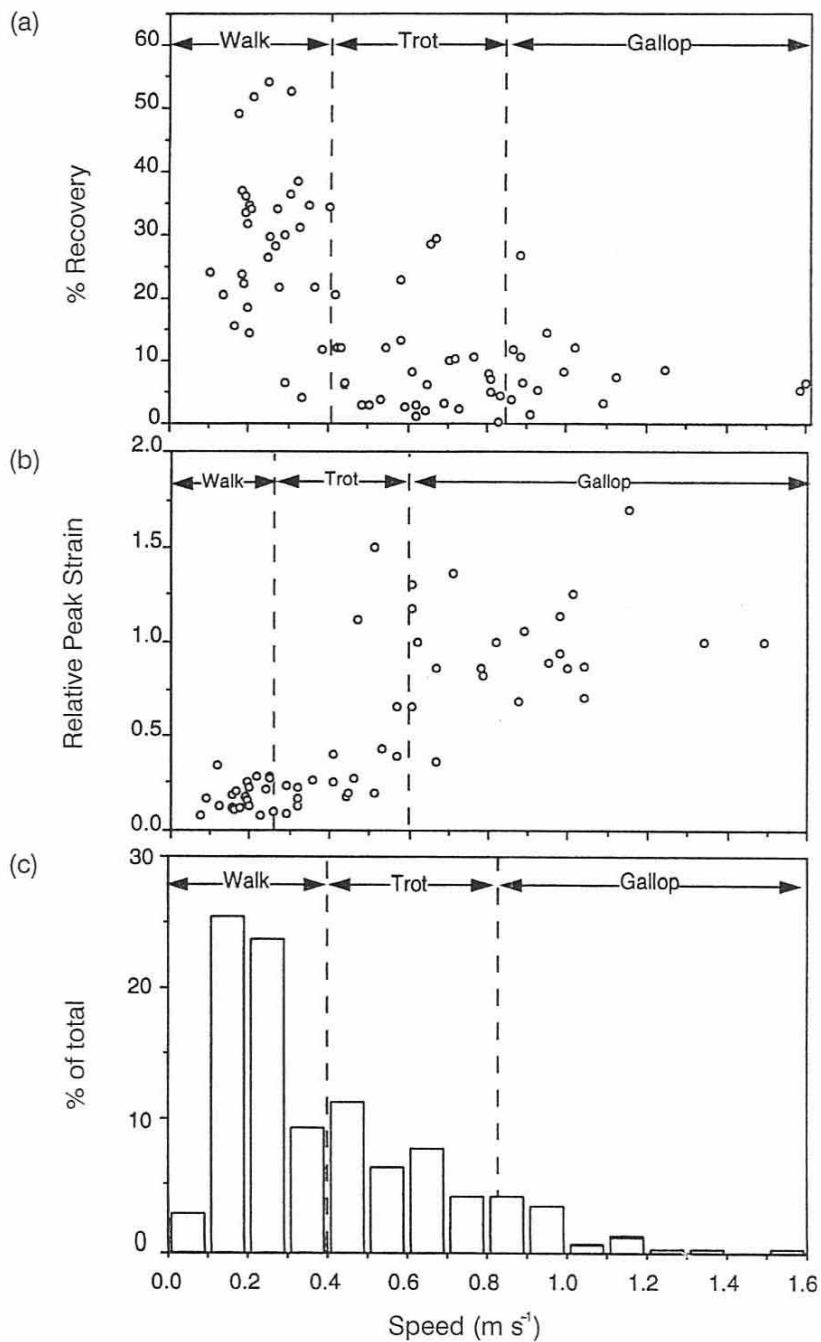
Stride frequency increases linearly with exercise speed in walking and trotting gaits and it becomes independent of speed at exercise speeds greater than  $0.8 \text{ m s}^{-1}$ . At these fast speeds, ghost crabs increase stride length and have an aerial phase (Blickhan and Full, 1987) and the gait is called a gallop. Relative peak strain in the exoskeleton during a gallop increases significantly over that observed in a walk or trot (*Figure 1(b)*; Blickhan *et al.*, 1993). To minimize the relative peak strain in the exoskeleton, ghost crabs should move continuously at speeds less than  $0.6 \text{ m s}^{-1}$ .

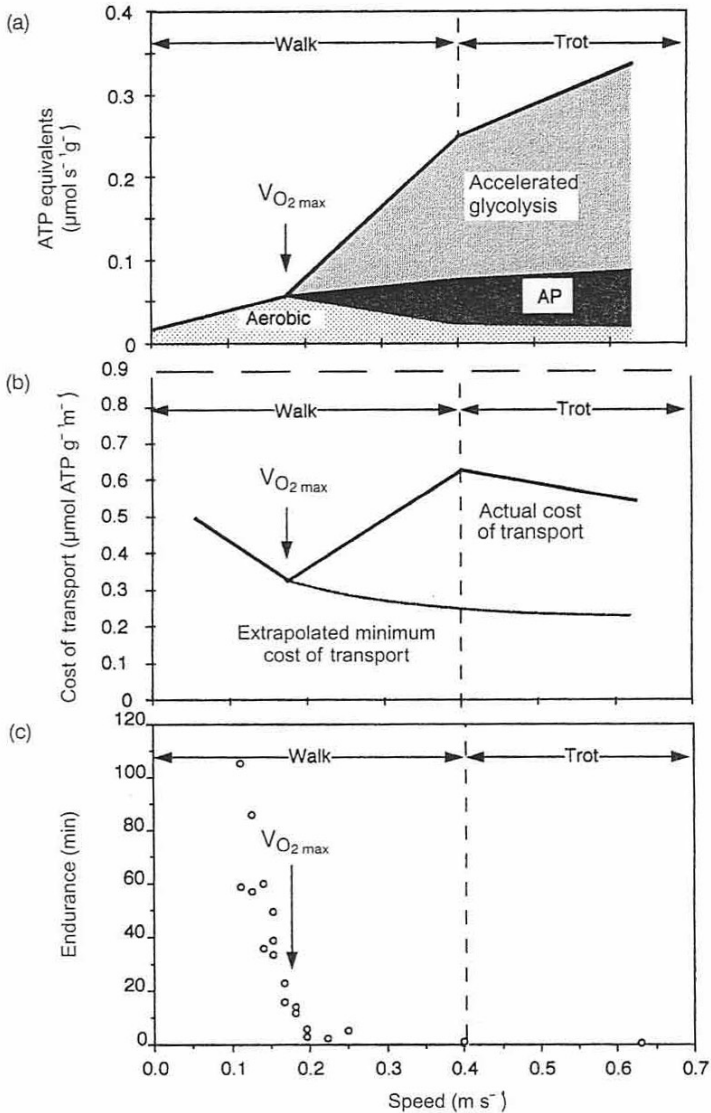
### 2.2 Energetics

During continuous terrestrial locomotion, steady-state oxygen consumption increases linearly with speed until a maximal rate of oxygen consumption is attained (*Figure 2(a)*). The slowest speed that elicits the maximal rate of oxygen consumption is the maximum aerobic speed (MAS; John-Alder and Bennett, 1981). At speeds below the MAS (i.e.  $< 0.2 \text{ m s}^{-1}$  for 30 g ghost crabs), the energy required for sustained, constant speed locomotion is supplied by aerobic ATP production. Ghost crabs can increase their rates of oxygen consumption as much as 12-fold greater than resting rates (Full and Herreid, 1983). Their aerobic factorial scope is comparable with that found in exercising mammals (five- to 15-fold; Taylor *et al.*, 1980). Accelerated glycolysis in ghost crabs contributes little to energy production during steady-state, submaximal exercise, even at speeds that elicit 70–90% of maximal rates of oxygen consumption (Full, 1987). At speeds above the MAS (i.e.  $> 0.2 \text{ m s}^{-1}$ ), ghost crabs rely heavily on nonaerobic sources (*Figure 2(a)*). For these experiments, crabs were exercised on a treadmill and then whole animals were frozen in liquid nitrogen. Lactate and arginine phosphate concentrations in walking legs were assayed spectrophotometrically. Crabs exercising at the walk–trot transition (i.e.  $0.4 \text{ m s}^{-1}$ ) show large increases in muscle lactate and a significant depletion of the high-energy phosphate, arginine phosphate

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*Figure 1. Biomechanics of continuous locomotion by the ghost crab. (a) Energy recovery as a function of speed and gait (Blickhan and Full, 1987). (b) Peak strain in the exoskeleton as a function of speed and gait (Blickhan et al., 1993). It should be noted that the gait transitions are shifted to lower speeds because the individuals in this study were of smaller mass. (c) Preferred speed of free locomotion by ghost crabs obtained on a track (Blickhan and Full, 1987). The preferred speed distribution attained a maximum in the middle of the walking gait where mechanical energy exchange is maximal and strain is minimized. It should be noted that speeds above the maximum aerobic speed ( $> 0.2 \text{ m s}^{-1}$ ) were frequent.*





**Figure 2.** Energetics and endurance of continuous locomotion by the ghost crab. (a) Aerobic, high-energy phosphate (AP) and glycolytic contributions to walking and trotting in ghost crabs (Full and Prestwich, 1986). Aerobic contributions decline at speeds above the maximal oxygen consumption ( $V_{O_2 \max}$ ) because oxygen uptake does not attain a steady state before fatigue. (b) Total cost of locomotion as a function of speed. The total cost includes high-energy phosphate (AP) and glycolytic contributions. The total cost of locomotion is minimized at the maximum aerobic speed. (c) Endurance or time to fatigue as a function of speed (Full, 1987). Endurance decreases to low values at speeds above the maximum aerobic speed. From Full and Weinstein (1992).

(Full and Prestwich, 1986). The rates of lactate accumulation and arginine phosphate depletion are even faster at speeds that fall in the middle of the trot (i.e.  $0.6 \text{ m s}^{-1}$ ). The contribution of ATP from aerobic metabolism may actually decrease at these high speeds because the crabs fatigue before attaining their maximal rate of oxygen consumption. The total energy utilization rate appears to increase curvilinearly as speed is increased (Full and Prestwich, 1986). To maximize the reliance on aerobic metabolism and minimize the contribution of nonaerobic energy sources, ghost crabs should move continuously at speeds of  $0.2 \text{ m s}^{-1}$  (i.e. the MAS).

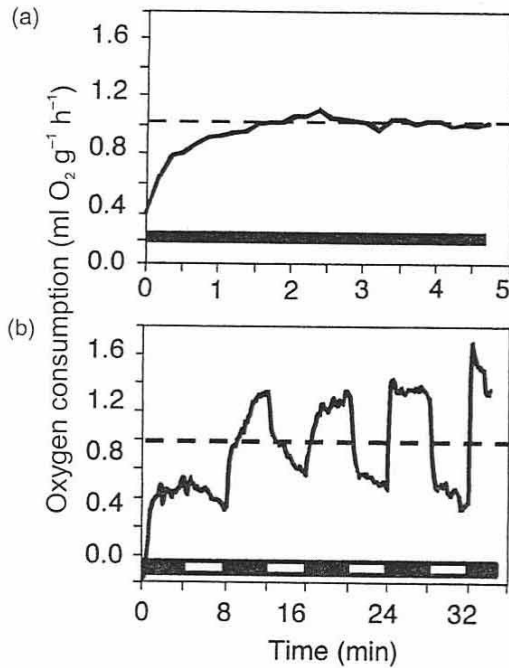
The metabolic cost to travel a given distance (i.e. the cost of transport) can be expressed as an aerobic or total cost of transport. The aerobic cost of transport, which is calculated from the amount of oxygen consumed per distance, decreases and approaches the minimum cost of locomotion (i.e.  $C_{\min}$ ) as exercise speed increases to approach the MAS. The  $C_{\min}$  is typically restricted to aerobically supported speed ranges (Heglund *et al.*, 1982; Taylor *et al.*, 1970). This speed range is narrow for ghost crabs and most other ectotherms relative to endotherms of the same body mass. If the total cost of transport, which is calculated from the total ATP consumed per distance and includes both aerobic and nonaerobic energy sources, is considered for ghost crabs, then an energetic minimum appears to be attained in the middle of the walking gait (i.e. at  $0.2 \text{ m s}^{-1}$ ; *Figure 2(b)*). To minimize the aerobic cost of transport, ghost crabs should move continuously at a speed equal to or greater than  $0.2 \text{ m s}^{-1}$ , provided that the exercise speed is aerobically sustainable. To minimize the total cost of transport, ghost crabs should move continuously at a speed of  $0.2 \text{ m s}^{-1}$ .

### 2.3 Endurance

Exercise at speeds below the MAS has been termed 'sustainable' because it can be maintained by aerobic metabolism. Exercise at speeds above the MAS requires supplemental energy provided by nonaerobic sources and is classified as 'nonsustainable', as it rapidly leads to exhaustion. Indeed, ghost crab endurance declines significantly at speeds above the MAS (*Figure 2(c)*; Full, 1987). The MAS determined in the laboratory has been used to predict the speed of animal locomotion in the field, leading to the general prediction that under natural conditions, animals travel at or below the MAS (Gleeson, 1979; Hertz *et al.*, 1988; John-Alder *et al.*, 1983). Using this criterion, ghost crabs should move continuously at speeds equal to or less than their maximum aerobic speed ( $0.2 \text{ m s}^{-1}$ ) to maximize endurance.

## 3. Predictions based on laboratory studies of non-steady-state locomotor behaviour

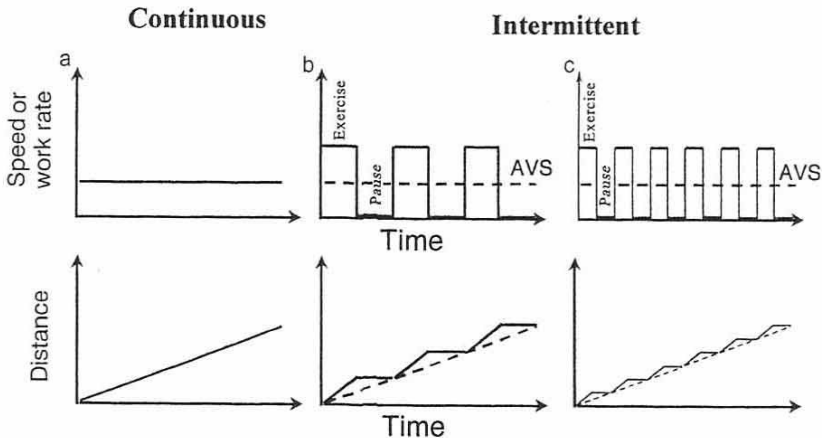
Although continuous, steady-state exercise has played an essential role in defining the limits of locomotor performance, steady-state conditions represent an artificial situation for many animals and the systems that support their activity. Few animals move continuously. Instead, most animals move intermittently – starting and stopping frequently. Energy demand, oxygen transport, and biomechanics of musculoskeletal systems are well documented during steady-state, constant speed locomotion. However, physiological and biomechanical systems must function under non-steady-state, transient conditions during intermittent activity (*Figure 3*). Therefore, we must re-evaluate the capacity of biomechanical and physiological systems with respect to



**Figure 3.** Oxygen uptake kinetics of ghost crabs as a function of time for continuous versus intermittent locomotion. (a) Continuous locomotion at a constant speed of  $0.15 \text{ m s}^{-1}$ . (b) Intermittent locomotion at a constant average speed of  $0.15 \text{ m s}^{-1}$ . Exercise periods were conducted at speeds of  $0.30 \text{ m s}^{-1}$  and interspersed with pause periods of zero speed. Protocols are shown with filled bars representing exercise and open bars pause periods. Modified from Weinstein and Full (1992). The average rate of oxygen consumption is shown by the dashed line.

repeated transitions to advance our understanding of systems design, function, and control. Furthermore, we should consider intermittent locomotor behaviour when we formulate predictions for performance in the field.

Intermittent exercise is defined by three variables: work duration, work rate, and pause duration. Locomotor speed is an indicator of the amount of mechanical work done by animals such as ghost crabs moving on land. The rate of mechanical energy required to move the center of mass increases linearly with speed (Blickhan and Full, 1987). Therefore, as a ghost crab moves faster it does more mechanical work. When a ghost crab travels at a constant work rate (e.g. at a constant speed), the distance it travels, calculated by integrating the speed function, increases linearly (*Figure 4(a)*). However, if the crab moves intermittently, alternating a brief work period with brief pause periods, the instantaneous work rate varies over time and the amount of work done (e.g. distance traveled) increases in a step-like manner (*Figure 4(b)*). The average work rate of a complete work–pause cycle is calculated from the absolute work rate during the work period and the duty cycle (per cent of complete work–pause cycle the animal spends moving). Thus, at the end of a complete work–pause cycle, the total

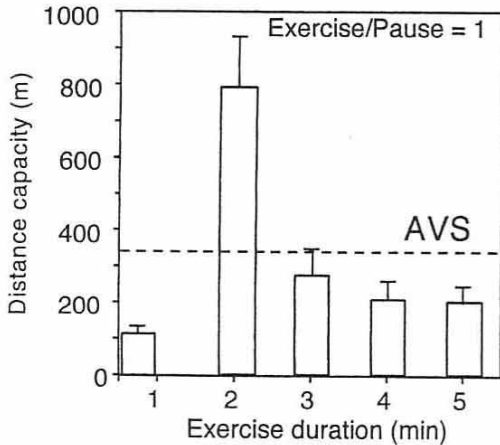


**Figure 4.** Comparison of continuous versus intermittent work. (a) Instantaneous work rate (or speed) and work (or distance) versus time for continuous locomotion. (b) Instantaneous work rate (or speed) and work (or distance) versus time for intermittent locomotion. The dashed line represents the same average continuous work rate or speed as shown in (a). (c) Instantaneous speed and distance versus time for intermittent locomotion at a shorter exercise and pause duration than in (b). Exercise and pause duration of intermittent locomotion can be varied while maintaining the same average speed or work rate. AVS, average speed.

work done during intermittent locomotion is the same as during continuous locomotion at the same average work rate. Intermittent protocols that differ in exercise duration, pause duration or instantaneous work rate can still lead to the same average work rate (Figure 4(c)).

### 3.1 Distance capacity

In cases where ghost crabs perform the work at the same average rate, we might predict similar endurance capacity. We find distance capacity, defined as the total distance traveled before fatigue (Weinstein and Full, 1992), to be a more useful measure of endurance capacity for intermittent exercise, as endurance usually implies continuous activity. Despite the same average work rates for continuous and intermittent movement, the frequent dynamic adjustments that characterize intermittent locomotion can alter distance capacity. When ghost crabs move intermittently, by alternating brief periods of exercise at a speed greater than the MAS with brief pauses, they can travel as much as two to five times farther before they fatigue than if they move continuously at the same submaximal average speed (Figure 5; Weinstein and Full, 1992, 1998). Alternatively, under different exercise and pause intervals, the distance capacity for intermittent locomotion can be reduced to a tenth that of continuous locomotion at the same average speed (Weinstein and Full, 1992). Ghost crabs moving at slow, 'sustainable' speeds (i.e. below the MAS) should be able to travel long distances before fatigue whether they move continuously or intermittently. Faster moving crabs should move intermittently to maximize distance capacity although not all movement-pause intervals will result in improved performance.



*Figure 5.* Distance capacity as a function of exercise and pause duration for the ghost crab. Distance capacity is defined as the distance traveled before fatigue. The ratio of exercise to pause duration was kept at one. Values are means  $\pm$  SE. All protocols yielded distance capacities that were significantly different from those for continuous locomotion at the same average speed (AVS) except for the 3 min exercise duration experiment. From Weinstein and Full (1992).

### 3.2 Energetics

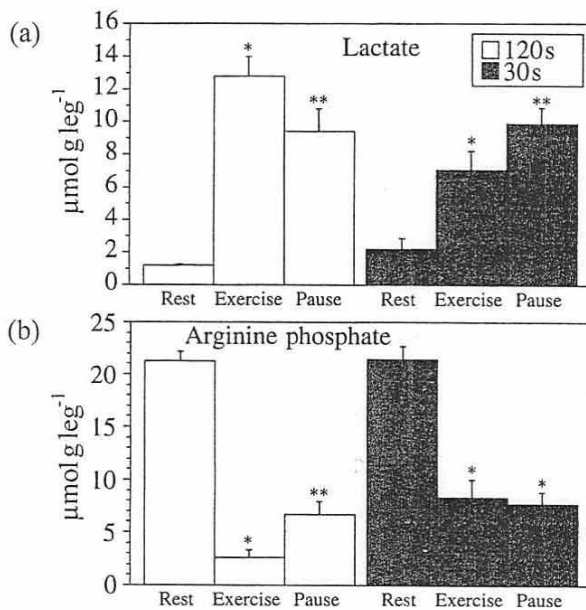
Predictions regarding the supply of ATP to working muscle during steady-state exercise do not predict the supply of ATP during intermittent exercise, which is characterized by frequent transitions from rest to exercise and vice versa (Figure 3). Whereas ATP for steady-state submaximal continuous exercise is derived primarily from oxidative metabolism, a significant non-negligible fraction of the total ATP must be derived from anaerobic metabolism during both submaximal and supramaximal intermittent exercise. If the exercise duration is shorter than the time to reach and sustain a steady-state rate of oxygen consumption, then ATP must be generated by nonoxidative pathways to meet the increased ATP demand. However, as short exercise bouts are alternated with brief pauses, there is a potential for at least partial recovery from metabolic fatigue.

The average aerobic cost of intermittent exercise is determined by integrating segments of the intermittent exercise records that contain at least one complete exercise-pause cycle in which the sum of the increase and decrease in oxygen consumption are within a constant percentage of the average oxygen consumption of the animal (Weinstein and Full, 1992). Whereas the average aerobic cost of intermittent locomotion is similar to or higher than the cost of continuous exercise at the same average speed (Weinstein and Full, 1992, 1998), the total metabolic cost of intermittent locomotion has yet to be addressed. As ghost crab muscles have elevated lactate and depleted high-energy phosphate stores at the end of a bout of intermittent exercise (Weinstein and Full 1992, 1998), the total metabolic cost of intermittent exercise should include both aerobic and anaerobic energy production. If anaerobic costs are added to aerobic costs, the total metabolic cost of intermittent exercise is



likely to be even greater than for continuous locomotion at the same average speed. Elevated muscle lactate in intermittently exercising Christmas Island red crabs (*Gecarcoidea natalis*) also supports an increased total cost for intermittent locomotion (Adamczewska and Morris, 1998). To minimize the total metabolic cost of intermittent locomotion per unit time, ghost crabs should move at submaximal speeds during the exercise intervals. Pauses should be adequate for at least partial recovery from fatigue incurred during the previous exercise period. In addition, the movement durations of fast-moving stressed crabs should be shorter than those of crabs moving at slow speeds to minimize fatigue associated with movement at rapid speeds.

In the laboratory, changes in ghost crab leg muscle metabolites are correlated with changes in whole-animal intermittent locomotor performance (Figure 6). Alternating 120 s of exercise periods with 120 s pause periods increases distance capacity by two-fold compared with continuous locomotion at the same average speed (Weinstein and Full, 1992). During a 120 s pause period, there is net clearance of lactate from leg



**Figure 6.** Metabolite changes in the ghost crab leg in response to intermittent locomotion. (a) Lactate for two intermittent exercise protocols during rest, at the end of exercise and at the end of a pause period. (b) Arginine phosphate for two intermittent exercise protocols. Open bars represent a 30 s exercise, 30 s pause protocol, which results in a decrease in distance capacity compared with continuous locomotion at the same average speed. Closed bars represent a 120 s exercise, 120 s pause protocol, which results in an increase in distance capacity compared with continuous locomotion at the same average speed. A single asterisk indicates a difference from rest. A double asterisk indicates a difference from rest and from the exercise group. The exercise speed was 160% MAS during exercise ( $0.3 \text{ m s}^{-1}$ ) for both protocols. The muscle samples were frozen at the end of the fourth exercise or pause period. From Weinstein and Full (1992; the 120 s data) and Full and Weinstein (1992; the 30 s data).

muscle and net resynthesis of arginine phosphate (Weinstein and Full, 1992). In contrast, intermittent exercise with 30 s exercise bouts alternated with 30 s pauses resulted in a decrease in distance capacity, no net clearance of lactate from leg muscle and no resynthesis of arginine phosphate during the pause period (Full and Weinstein, 1992).

#### 4. Testing laboratory-based predictions from mechanics and energetics by measuring locomotor behaviour in the field

Laboratory studies of ghost crab biomechanics and energetics defined performance limits for continuous and intermittent locomotion and generated specific predictions for locomotor behaviour in the field. To determine where ghost crabs naturally operate within these performance limits, an IR videotaping system and focal animal sampling were used to observe ghost crabs in the field (Weinstein, 1995).

As predicted by laboratory studies of continuous locomotor performance limits, ghost crabs generally moved at speeds below their MAS. During routine foraging behaviour, voluntarily active crabs move at a mean instantaneous velocity of  $0.08 \text{ m s}^{-1}$ , as measured by three-dimensional motion analysis (Weinstein, 1995). The mean stride frequency of voluntarily active focal animals ( $2.1 \text{ strides s}^{-1}$ ) is equivalent to a velocity of about  $0.1 \text{ m s}^{-1}$  (Blickhan and Full, 1987). Therefore, most of the time, voluntarily active ghost crabs move at speeds below their MAS of approximately  $0.2 \text{ m s}^{-1}$  (Full, 1987). Mechanically, these voluntarily active ghost crabs primarily use a walking gait, as the mean stride frequency is less than the stride frequency at the walk-run transition (about  $4 \text{ strides s}^{-1}$ ; Blickhan and Full, 1987). The metabolic energy for these slow speeds is probably supplied by aerobic metabolism and although lactate concentrations were not measured in the field, they are likely to be close to resting levels (Full, 1987). A ghost crab moving continuously at  $0.08 \text{ m s}^{-1}$ , a speed that is 46% of its MAS, will have an endurance capacity of more than 2 h (body temperature  $24^\circ\text{C}$ ; Full, 1987).

Intermittent locomotion is not likely to alter the voluntarily active ghost crab's distance capacity at the slow speeds measured in the field. The mean movement duration is 11 s and the mean pause duration is 23 s (Weinstein, 1995). If the ghost crab moves intermittently, alternating 11 s of movement at  $0.08 \text{ m s}^{-1}$  with 23 s pause periods, the average speed is only  $0.03 \text{ m s}^{-1}$  (15% MAS). The endurance capacity for continuous exercise at  $0.03 \text{ m s}^{-1}$  is greater than 2 h (Full, 1987). Starting and stopping frequently may increase the metabolic cost of movement at these slow speeds, but is not likely to constrain the ghost crab's distance capacity.

Stressed crabs, such as those escaping from predators or incoming waves and engaging in intra-specific aggression, move at speeds greater than their MAS. Stressed crabs move with a mean instantaneous velocity of  $0.83 \text{ m s}^{-1}$ , as determined by three-dimensional motion analysis (Weinstein, 1995). Mechanically, stressed crabs move at speeds that correspond to a running gait, as the stride frequency estimated from the mean instantaneous velocity is greater than the stride frequency at the walk-run transition (Blickhan and Full, 1987). The rapid movements of the stressed crabs cannot be supported aerobically and require additional energy from nonoxidative energy sources. Lactate levels of these stressed crabs are likely to be elevated above resting levels (Full, 1987). Endurance capacity for continuous exercise at  $0.83 \text{ m s}^{-1}$  is less than 10 s, corresponding to a distance of less than 2 m (Full, 1987; Full and Prestwich, 1986). Despite the low endurance capacity for continuous exercise at the mean instantaneous velocities measured in the

field, the stressed crabs moved over distances greater than 2 m, yet they did not appear to be completely fatigued (i.e. subsequent movements were observed following brief pauses; Weinstein, 1995). Stressed ghost crabs behave differently from voluntarily active crabs. The stressed crabs alternate 1–2 s movement periods with 8 s pause periods, resulting in an average speed of only  $0.13 \text{ m s}^{-1}$  (65% MAS). Endurance capacity for continuous locomotion at  $0.13 \text{ m s}^{-1}$  is approximately 55 min, corresponding to a total distance of 410 m. The greater distance capacity observed in the field, compared with the predicted distance capacity based on continuous locomotion, suggests that the performance limits of the stressed crabs are increased as a result of intermittent movement. The long pause period duration, relative to the short movement duration, may allow the stressed crabs to partially recover from their brief, high-intensity movements and may explain their increased performance capacity.

## 5. Generality of the consequences of intermittent locomotor behaviour in other ectotherms

Because oxygen transport kinetics appears to play an important role in determining the effect of intermittent locomotion, we selected species that differ in their oxygen uptake kinetics (Table 1). We chose the American cockroach, *Periplaneta americana*, because it possesses very rapid onset kinetics and can increase oxygen consumption 20-fold over resting levels (Herreid and Full, 1984). Furthermore, *P. americana* does not accumulate significant anaerobic end-products such as lactate or  $\alpha$ -glycerophosphate at speeds exceeding the MAS (Full and Min, 1990). We hypothesized that intermittent locomotion should have little or no effect on distance capacity for highly aerobic species with rapid kinetics such as *P. americana*. To ensure that our findings are not specific to insects because of some unique character such as tracheae, we also examined several other species with differing oxygen uptake kinetics, including the hissing cockroach, *Gromphadorhina portentosa*, which does accumulate a significant amount of lactate during exercise at speeds greater than the MAS (Lee *et al.*, 1993). We hypothesized that intermittent locomotion in *G. portentosa* should alter distance capacity under particular exercise–pause regimes just as it does in other invertebrate species with moderate oxygen uptake kinetics, such as the ghost crab, *O. quadrata*, and in some lower vertebrates such as the frog-eyed gecko, *Teratoscincus przewalskii* (Autumn *et al.*, 1994; Weinstein and Full, 1999). We also examined the effect of intermittent locomotion in the highly anaerobic fiddler crab, *Uca pugilator*, which relies heavily on anaerobic metabolism to move at the slowest walking speeds (Full and Herreid, 1984). We hypothesized that intermittent locomotion should have the greatest effect on *U. pugilator*, as it could benefit most by recovering during frequent pauses.

### 5.1 Fast oxygen uptake kinetics (American cockroaches)

As we predicted, intermittent locomotion did not increase distance capacity in *P. americana* (Table 1; Lee *et al.*, 1992). The distance capacity for *P. americana* exercising intermittently did not differ significantly from that for continuous exercise at the same average speed when the exercise speed was 150% MAS, the exercise–pause ratio was 1.0 (duty cycle 50%), and the exercise duration was 15 or 30 s (Table 2). However, intermittent exercise resulted in a 25% decrease in distance capacity compared with continuous exercise at the same average speed when the exercise speed was 143%

**Table 1.** Comparison of continuous and intermittent locomotor performance in species with different oxygen uptake kinetics

Species	$t_{1/2on}$ (s)	Factorial aerobic scope ( $V_{O_{2max}}/V_{O_{2rest}}$ )	Maximum % change in distance capacity relative to continuous exercise at same average speed
American cockroach ( <i>P. americana</i> <sup>a</sup> )	<30	29	-25
Hissing cockroach ( <i>G. portentosa</i> <sup>b</sup> )	60	16	+92
Ghost crab ( <i>O. quadrata</i> <sup>c</sup> )	29	10	+119
Gecko ( <i>T. przewalskii</i> <sup>d</sup> )	83	5	+67
Fiddler crab ( <i>U. pugilator</i> <sup>e</sup> )	120	5	-65

$t_{1/2on}$ , time to reach 50% of the steady-state rate of oxygen consumption;  $V_{O_{2max}}$ , maximal rate of oxygen consumption,  $V_{O_{2rest}}$ , resting rate of oxygen consumption. <sup>a</sup>Lee *et al.* (1992); <sup>b</sup>Lee *et al.* (1993); <sup>c</sup>Weinstein and Full (1992); <sup>d</sup>Weinstein and Full (1999); <sup>e</sup>Van Laarhoven *et al.* (1993).

**Table 2.** Comparison of distance capacity for continuous and intermittent exercise at the same average speed in several ectothermic species

Species	Exercise duration (s)	Pause duration (s)	Average speed (% MAS)	Absolute speed (% MAS)	Maximum % change in distance capacity relative to continuous exercise at same average speed
American cockroach ( <i>P. americana</i> <sup>a</sup> )	15	15	75	150	NS
	30	30	75	150	NS
	10	5	95	143	-25
Hissing cockroach ( <i>G. portentosa</i> <sup>b</sup> )	5	5	90	180	+92
	10	5	90	135	+72
	30	15	90	135	+59
	15	15	90	180	-15
Ghost crab ( <i>O. quadrata</i> <sup>c</sup> )	120	120	83	166	+119
	30	30	83	166	-71
Gecko ( <i>T. przewalskii</i> <sup>d</sup> )	15	30	90	270	+67
	30	30	90	180	NS
	120	120	90	180	NS
Fiddler crab ( <i>U. pugilator</i> <sup>e</sup> )	9	3	85	113	NS
	10	10	85	170	-65

MAS, maximum aerobic speed; NS, not significantly different from continuous exercise at the same average speed. <sup>a</sup>Lee *et al.* (1992); <sup>b</sup>Lee *et al.* (1993); <sup>c</sup>Weinstein and Full (1992); <sup>d</sup>Weinstein and Full (1999); <sup>e</sup>Van Laarhoven *et al.* (1993).

MAS, the exercise duration was 10 s and the pause duration was 5 s (duty cycle 66%). The average aerobic cost of intermittent exercise was not significantly different from the corresponding values for continuous exercise at the same average speed for any of the intermittent exercise protocols.

### 5.2 Moderate oxygen uptake kinetics (hissing cockroaches, ghost crabs, and frog-eyed geckos)

Moving intermittently increased distance capacity in species with moderate oxygen uptake kinetics, including the ghost crab (Table 1; Weinstein and Full, 1992). For *G. portentosa*, three intermittent exercise protocols increased distance capacity and one decreased distance capacity compared with continuous exercise at the same average speed (90% MAS; Lee *et al.*, 1993). When the exercise speed was 180% MAS, the exercise-pause ratio was 1.0 (duty cycle 50%), and the exercise duration was 5 s; intermittent exercise increased distance capacity by 92% compared with continuous locomotion at the same average speed (Table 2). Alternating 30 s of exercise at 135% MAS with 15 s pauses, or 10 s of exercise at 135% MAS with 5 s pauses (duty cycle 66%), increased distance capacity by 59–72% compared with continuous locomotion at the same average speed. Intermittent exercise decreased distance capacity by 15% compared with continuous exercise at the same average speed when the exercise speed was 180% MAS, the exercise duration was 15 s, and the pause duration was 15 s (duty cycle 50%). The average aerobic cost of intermittent exercise was not significantly different from the corresponding values for continuous exercise at the same average speed for any of the intermittent exercise protocols.

At an absolute exercise speed of 270% MAS, *T. przewalskii* exercising intermittently with a 15 s exercise duration and a 30 s pause duration (duty cycle 33%) exhibited an 11-fold increase in distance capacity compared with lizards exercised continuously at the same absolute speed (270% MAS) and a 67% increase in distance capacity compared with geckos exercised continuously at the same average speed (90% MAS; Table 1; Weinstein and Full, 1999). At an exercise speed of 180% MAS, geckos alternating 30 s exercise periods with 30 s pause periods or 120 s exercise periods with 120 s pause periods (duty cycle 50%) had similar distance capacities compared with geckos exercising continuously at the same average speed (90% MAS; Table 2). The average aerobic cost of intermittent exercise for *T. przewalskii* was not significantly different from the maximal rate of oxygen consumption.

### 5.3 Slow oxygen uptake kinetics (fiddler crabs)

Contrary to our prediction, intermittent locomotion reduced or did not alter distance capacity in *U. pugilator* (Table 1; Van Laarhoven *et al.*, 1993). When fiddler crabs alternated 10 s of exercise at 170% MAS with 10 s pauses (duty cycle 50%), distance capacity was reduced by 65% compared with continuous locomotion at the same average speed (85% MAS; Table 2). In the field, the average movement duration of droving *U. pugilator* was 9 s and the average pause duration was 3 s (duty cycle 66%; Weinstein, 1993). When these intervals were tested in the laboratory, the distance capacity for intermittent locomotion was not significantly different from that for continuous locomotion at the same average speed (85% MAS; Van Laarhoven *et al.*, 1993). The average aerobic cost of intermittent exercise was not significantly different

from the corresponding values for continuous exercise at the same average speed for any of the intermittent exercise protocols.

## 6. Conclusion

The total amount of work performed during a behaviour depends on the rate at which the work is done, the duration of the work, and the extent to which the behaviour is conducted intermittently. Low work rate behaviours performed continuously can be sustained for long periods of time, resulting in substantial amounts of total work. High work rate behaviours performed continuously can be sustained only for short periods of time, allowing only small amounts of total work to be accomplished. Surprisingly, if a high work rate behaviour is performed intermittently, the total work accomplished can far exceed the work done during the same behaviour performed continuously at the same average work rate. Intermittent locomotor behaviour appears to have its greatest effect on species that rely on both aerobic and nonaerobic energy sources. Highly aerobic or nonaerobic species are affected less by the intermittent nature of the behaviour. Clearly, the biomechanics of behaviour must be considered in the context of the animal's physiological capacity.

Many behaviours involve intermittent activity. Intermittent locomotion, also called stop-and-go or saltatory search behaviour by ethologists, can improve prey detection by providing predators with more time to scan a given visual field (Andersson, 1981; Avery, 1993; Avery *et al.*, 1987; Gendron and Staddon, 1983), reduce the rate of attack by predators (Martel and Dill, 1995), and improve detection of predators (McAdam and Kramer, 1998). No matter what the advantage of an intermittent behaviour may be, the ability of an animal to sustain the performance of the behaviour will be determined by its physiological capacity and biomechanical limitations.

Finally, we contend that non-steady-state behaviour involving transitions must be afforded the same degree of attention as given to the steady-state behaviour. Perhaps the design of musculoskeletal, circulatory and respiratory systems is determined primarily by non-steady-state behaviour. These further studies of intermittent locomotion could lead to improved predictions of field behaviour. At the same time, a knowledge of field behaviour can set the biomechanical and physiological protocols by which we test future hypotheses of function.

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