Intermittent exercise alters endurance in an eight-legged ectotherm

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Weinstein, Randi B., and Robert J. Full. Intermittent exercise alters endurance in an eight-legged ectotherm. Am. J. Physiol. 262 (Regulatory Integrative Comp. Physiol. 31): R852-R859, 1992.—Most animals move intermittently, yet many proposed performance limitations of terrestrial locomotor systems are based on steady-state locomotor performance and assumptions. We examined the effect of work-rest transitions by exercising the ghost crab, Ocypode quadrata (28.1 ± 8.1 g), intermittently on a treadmill at 0.30 m/s, a supramaximal speed (i.e., greater than the speed that elicits the maximal rate of oxygen consumption \( \text{V} \text{O}_2 \)). Duration of the exercise and pause periods, ratio of exercise to pause, and speed during the exercise period were varied to determine the effect on performance. Crabs fatigued after 7.5 min of continuous running, a distance capacity (i.e., total distance traveled before fatigue) of 135 m. When the task was done intermittently with 2-min exercise and 2-min pause periods, the crabs fatigued after 97 min (a total distance of 787 m), representing a 5.8-fold increase in distance capacity compared with continuous exercise at the same absolute speed (0.30 m/s) and a 2.2-fold increase in distance capacity compared with continuous exercise at the same average speed. Pausing periods <30 s did not result in greater distance capacity compared with continuous exercise at the same average speed. Longer (3–5 min) and shorter exercise periods (<30 s) decreased distance capacity. Leg muscle lactate increased 10-fold to 15 \( \mu \text{mol/g} \) leg during intermittent exercise. However, significant amounts of lactate were cleared from the leg during the brief pause periods. The average \( \text{V} \text{O}_2 \) during intermittent exercise was not statistically different from maximal \( \text{V} \text{O}_2 \). The aerobic cost of intermittent exercise, both per time and per distance, was equal to or greater than the aerobic cost of continuous exercise at the same average speed. Further examination of dynamic physiological adjustments, such as in intermittent exercise, is likely to alter the performance limits established under a steady-state paradigm.

Oxygen consumption; muscle; lactate; arthropods

STABLE-OXYGEN CONSUMPTION \( (\text{V} \text{O}_2) \) increases with speed during constant-speed terrestrial locomotion until a maximal rate of consumption \( \text{V} \text{O}_2 \text{max} \) is attained. Endurance of continuous locomotion has been shown to be correlated with the maximal capacities of an animal for aerobic metabolism (4). Body size (36, 55), body temperature (39, 40), and the metabolic cost of locomotion (23) all affect \( \text{V} \text{O}_2 \text{max} \) or the speed at which it is attained (i.e., maximum aerobic speed (MAS) (39)). Exercise at speeds below the MAS (i.e., submaximal speeds) is considered sustainable and can be maintained by aerobic metabolism. Locomotion at speeds greater than MAS (i.e., supramaximal speeds) requires supplemental energy provided by anaerobic metabolism and is considered unsustainable, because it rapidly leads to exhaustion. In mammals (55), lizards (39, 40), salamanders (20), and crabs (31), endurance declines considerably at speeds approaching the MAS.

Results from studies on constant-speed steady-state exercise have been used 1) to develop design principles for oxygen and energy transport (57), 2) to advance hypotheses concerning the evolution of endothermy (6), and 3) to predict natural locomotor behavior (5, 37). However, steady-state continuous exercise could represent "an artificial situation for many animals" (2) and the systems that support activity. Few animals move continuously. Most animals start and stop; that is, they move intermittently. Studies of intermittent exercise indicate that alternating periods of high-intensity exercise with pause periods, during which low-intensity or no work is done, can alter metabolic reactions and endurance (52). Early studies of intermittent exercise on humans showed that when a heavy (i.e., supramaximal) work load was divided into short exercise and pause periods, the heavy work load was "transformed to a submaximal load on circulation and respiration and could be well tolerated" (1). The duration of the exercise and pause periods had profound effects on endurance and lactate accumulation (13, 14). Significant lactate accumulation and phosphagen depletion in humans can be prevented by performing intermittent exercise with short exercise periods (i.e., <30 s) and longer pause periods (16, 19, 44, 51).

These previous studies lead us to propose that examination of intermittent locomotion and dynamic physiological adjustments should be the next paradigm used to evaluate the performance limits of oxygen and energy transport systems in exercising animals. Moreover, use of intermittent protocols could be used to improve predictions of natural locomotor behavior previously derived from steady-state tests.

In the present study we examine the effect of intermittent exercise on the performance of an eight-legged ectotherm. We selected the ghost crab, Ocypode quadrata, for several reasons. First, the ghost crab has a low \( \text{V} \text{O}_2 \text{max} \) and MAS relative to endotherms. The MAS for the ghost crab is a walking speed and reflects the inability of the ghost crab to sustain even a fast walking pace (8, 21). We hypothesize that intermittent locomotion will be of greater consequence in ectotherms and may represent a behavior that either reduces the limitations associated with a low \( \text{V} \text{O}_2 \text{max} \) and MAS or imposes additional constraints. Second, much is known about the ghost crab's locomotor performance with respect to biomechanics, energetics, endurance, and muscle biochemistry (8, 21, 26, 27). Third, observations of ghost crabs in their natural habitat suggest that these active animals move intermittently, making frequent starts and stops rather than moving continuously for long distances along the beach (T. G. Wolcott, personal communication). Finally, several studies have been published on the continuous steady-state exercise performance of the ghost crab (8, 21, 24), and we have access to the same population of crabs used in these studies.

MATERIALS AND METHODS

Animals

The ghost crab, O. quadrata (28.1 ± 8.1 (SD) g), was collected from the beaches surrounding the Duke University Marine Laboratory in Beaufort, NC. Individual crabs were housed in plastic
containers filled with 30-50% seawater to a depth of 1 cm. The animals were kept in an environmental chamber on an 14:10 h light-dark photoperiod at 25°C. The crabs were fed fresh fish two or three times a week, and their containers were cleaned and filled with fresh seawater 24 h after feeding. Only intermictotrophic crabs were used. Individuals were kept in captivity <8 wk. To maximize the number of experimental trials, crabs were randomly assigned to three or four exercise groups (see below). As a result, no individual exercised at all protocols. Each individual rested for at least 5 days between trials.

**Vo2 and Distance Capacity Protocol**

Resting Vo2. Vo2 was measured as the crabs rested quietly in a treadmill respirimeter for 30 min. Metabolic rate was determined for 10 min before each exercise trial. The Vo2 value during the final 6 min of the 10 min exercise period was averaged to obtain the resting Vo2 (Vo2rest). All trials were conducted at 25°C.

Continuous exercise. The treadmill speeds selected for the present study were based on previous investigations of O. quadrata (21). Crabs were exercised continuously to fatigue on a treadmill at 0.3 or 0.4 m/s. A speed of 0.15 m/s elicits Vo2max and is therefore the MAS for these crabs (21). The speeds selected for continuous exercise, 0.30 (170% MAS) and 0.40 m/s (220% MAS), exceed MAS and were supermaximal. Measurements of Vo2max, MAS, and endurance during continuous exercise on crabs from the present study were not significantly different from those reported previously (21). The population of ghost crabs used in the present study was from the same crab population used by Full (21).

Intermittent exercise. Crabs exercised intermittently to fatigue by alternating exercise periods with rest periods. Four variables were manipulated in the intermittent exercise trials: 1) exercise duration (E), 2) pause duration (P), 3) E-to-P ratio, and 4) speed during the exercise period. Intermittent exercise protocols are outlined in Table 1 and include the corresponding absolute (Abs) and average speeds (AvS) for comparison with continuous exercise.

**Vo2 Measurements**

Crabs were exercised in a miniature treadmill respirimeter. Air flow rate was 500 ml/min. Air leaving the chamber was dried with calcium sulfate (Drierite), and CO2 was removed with asbestos (Ascarite). The oxygen concentration was monitored with an O2 analyzer (Ametek S3A), which was interfaced with a personal computer (Macintosh II) by data acquisition hardware and software (LabView, National Instruments). Mass-specific Vo2 was calculated from the O2 concentration (35). Calculations of instantaneous Vo2 (21, 36) were not significantly different from rates determined without the correction (58). Measurements of Vo2 were only made for the exercise protocols where the exercise period was at least 120 s.

**Distance Capacity Measurements**

Crabs were considered to be fatigued when they could no longer keep pace with the treadmill belt, even when prodded (21). Data from trials during which crabs walked erratically were discarded. Distance capacity (i.e., the total distance traveled continuously or intermittently before fatigue) was used as the index of endurance, instead of time to fatigue, because the term endurance usually connotes only continuous activity. The distance capacity for each trial was calculated from the treadmill speed and the number and duration of exercise intervals completed. The distance capacity for intermittent exercise was compared with continuous exercise at the same AbbS used during the exercise intervals and with continuous exercise at the same AvS.

**Muscle Lactate Protocol and Measurements**

After the Vo2 and distance capacity measurements were made, crabs were divided into four groups: rest (R), continuous exercise (CE), intermittent exercise (IE), and intermittent exercise pause (IP; Fig. 1). In the R group, animals rested in the treadmill chamber for 30 min before being frozen in liquid nitrogen. The CE group of crabs was exercised continuously to fatigue on the treadmill at 0.30 m/s and then was immediately frozen in liquid nitrogen. The IE protocol consisted of 2-min exercise periods (speed 0.30 m/s) alternated with 2-min pause periods. The crabs in the IE group were frozen in liquid nitrogen upon completion of the fourth exercise period. Crabs in the IP group were frozen at the end of the fourth pause period. Running direction was recorded to document whether legs were leading or trailing because the crabs ran sideways.

Whole animals were frozen rapidly (i.e., <2 s) in liquid nitrogen and stored at -80°C for <2 wk before tissue preparation and analysis. Leading and trailing third walking legs, along with the associated extrinsic musculature (i.e., within the body), were dissected free in a cold room (-5°C) and immediately homogenized in 4 vol of perchloric acid. After centrifugation the resulting supernatant was neutralized with K2CO3. Lactate concentration was determined according to Full and Herrell (25) with modifications from Prestwich (49).

**Statistical Analysis**

Unless noted, values are reported as means ± SE.

**Distance capacity. Statistical comparisons at submaximal AvS values were made by comparing 95% confidence intervals.**

**Table 1. Intermittent exercise protocols**

<table>
<thead>
<tr>
<th>Protocol No.</th>
<th>Exercise Period</th>
<th>Pause Period</th>
<th>Exercise-to-Pause Period Ratio</th>
<th>AbbS, m/s</th>
<th>AvS, m/s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant ratio</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>30</td>
<td>30</td>
<td>1</td>
<td>0.30</td>
<td>0.15</td>
</tr>
<tr>
<td>2</td>
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<td>120</td>
<td>1</td>
<td>0.30</td>
<td>0.15</td>
</tr>
<tr>
<td>3</td>
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<td>180</td>
<td>1</td>
<td>0.30</td>
<td>0.15</td>
</tr>
<tr>
<td>4</td>
<td>240</td>
<td>240</td>
<td>1</td>
<td>0.30</td>
<td>0.15</td>
</tr>
<tr>
<td>5</td>
<td>300</td>
<td>300</td>
<td>1</td>
<td>0.30</td>
<td>0.15</td>
</tr>
<tr>
<td>Varied pause duration</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>120</td>
<td>30</td>
<td>4</td>
<td>0.30</td>
<td>0.23</td>
</tr>
<tr>
<td>7</td>
<td>120</td>
<td>60</td>
<td>2</td>
<td>0.30</td>
<td>0.19</td>
</tr>
<tr>
<td>8</td>
<td>120</td>
<td>120</td>
<td>1</td>
<td>0.30</td>
<td>0.15</td>
</tr>
<tr>
<td>9</td>
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<td>5</td>
<td>6</td>
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<td>0.25</td>
</tr>
<tr>
<td>10</td>
<td>30</td>
<td>15</td>
<td>2</td>
<td>0.30</td>
<td>0.19</td>
</tr>
<tr>
<td>11</td>
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<td>0.5</td>
<td>0.30</td>
<td>0.10</td>
</tr>
<tr>
<td>12</td>
<td>5</td>
<td>10</td>
<td>0.5</td>
<td>0.30</td>
<td>0.10</td>
</tr>
</tbody>
</table>

AbbS, absolute speed (i.e., speed during exercise period); AvS, average speed for a complete exercise-pause cycle.

Fig. 1. Muscle metabolite protocol. Stippled bars, exercise periods; open bars, pause periods. Speed during exercise intervals was 0.30 m/s. Experimental groups are indicated by arrows: n = 6 crabs/group. R, rest group; CE, continuous exercise group; IE, intermittent exercise group; IP, intermittent pause group. Samples were taken after 30 min rest within the chamber (R), after continuous exercise to fatigue (CE), after the 4th intermittent exercise period (IE), and after the 4th intermittent pause period (IP).
for the total distance covered before fatigue during intermittent exercise with the 95% confidence intervals for the total distance covered before fatigue during continuous exercise at the same submaximal A/V S values. For the comparison at 0.30 m/s, a two-tailed Mann-Whitney U test was performed.

Aerobic cost. We performed analysis of variance to determine the effect of experimental condition. For comparisons between treatments we used Scheffé's F test.

Muscle lactate. We performed an analysis of variance to determine the effect of the experimental condition on muscle lactate concentration. For comparisons between treatments we used Scheffé’s F test. A paired t test was conducted to determine differences between leading and trailing legs within each condition.

RESULTS

\( \text{VO}_{2} \) 

\( \text{VO}_{2\text{rest}} \): \( \text{VO}_{2\text{rest}} \) at 25°C was 0.18 ± 0.05 ml O\(_2\)·g\(^{-1}\)·h\(^{-1}\) (n = 5). This resting rate was not significantly different from data collected by Full (21).

Continuous exercise. After the onset of exercise, \( \text{VO}_{2} \) increased rapidly to a steady state (\( \text{VO}_{2\text{ss}} \); Fig. 2A). The time to attain 50% of the \( \text{VO}_{2\text{ss}} \) (\( t_{1/2\text{on}} \)) was 38.5 ± 7.8 s (n = 4). This value for \( t_{1/2\text{on}} \) was not significantly different from data collected by Full (21), where \( t_{1/2\text{on}} \) was 28.2 s.

Intermittent exercise. For crabs exercising intermittently, \( \text{VO}_{2} \) increased as the crab exercised and decreased as the crab paused (Fig. 2, B and C). Longer exercise and pause periods resulted in greater oscillations in \( \text{VO}_{2} \). Exercise intervals lasting ≥2 min tended to result in a steady state. Even the longest pause periods, 6 min, did not result in complete aerobic recovery (i.e., \( \text{VO}_{2} \) did not return to \( \text{VO}_{2\text{rest}} \)).

Aerobic Cost of Exercise

The average aerobic cost of intermittent exercise was determined by integrating segments of the intermittent exercise record that contained at least one complete exercise-pause cycle in which the sum of the increase and decrease in \( \text{VO}_{2} \) were within a constant percentage of the average \( \text{VO}_{2} \) of the animal. This average \( \text{VO}_{2} \) (aerobic cost) was expressed both per unit time (ml O\(_2\)·g\(^{-1}\)·h\(^{-1}\)) and per distance (ml O\(_2\)·g\(^{-1}\)·km\(^{-1}\)).

Aerobic cost per time. For continuous exercise, \( \text{VO}_{2\text{ss}} \) increases linearly as exercise speed increases [Fig. 3A (21)]. At 0.18 m/s, the crab attained its \( \text{VO}_{2\text{max}} \), and further increases in speed did not result in subsequent

Fig. 2. Oxygen consumption (\( \text{VO}_{2} \)) kinetics for continuous (A) and intermittent (B and C) exercise for 3 different individuals. Exercise protocols are indicated on each graph as exercise periods (stippled bars) and pause periods (open bars). Dashed lines represent values for average \( \text{VO}_{2} \).

Fig. 3. A: average mass-specific \( \text{VO}_{2} \) or aerobic cost per time as a function of average speed. Values are means ± SE. Solid line shows previous data for ghost crabs (mass 26.9 ± 0.7 g) exercising continuously (21). At submaximal speeds, 95% confidence intervals are included. Exercise protocols are indicated by numerals and correspond to protocols outlined in Table 1. Sample sizes are as follows: protocols 2 and 13, n = 5; protocols 6 and 7, n = 4; protocols 3 and 4, n = 3; and protocol 5, n = 2. \( \text{VO}_{2\text{max}} \) : maximal \( \text{VO}_{2}\); B: average mass-specific aerobic cost per distance as a function of average speed. Solid line represents aerobic cost of locomotion per distance for crabs exercising continuously (21). Exercise protocols and sample sizes as in A.
increases in \( V_{O_2\text{max}} \). The average aerobic cost per time of intermittent exercise was independent of the AvS \((F_{1,19} = 0.41, P = 0.87, \text{Fig. 3A})\) and was not significantly different from \( V_{O_2\text{max}} \). The average aerobic cost per time for the 2-min E/2-min P protocol was significantly greater than the corresponding values for continuous exercise at the same AvS \((P < 0.05)\) but was not significantly different from rates of other intermittent exercise protocols.

**Aerobic cost per distance.** The average aerobic cost per distance of intermittent exercise decreases as the speed of the exercise period increases and approaches the minimum cost of locomotion \([C_{\text{min}}; \text{Fig. 3B (21)}]\). \( C_{\text{min}} \) is defined as the slope of the regression line from the plot of \( V_{O_2\text{max}} \) vs. speed \((36)\) and represents the minimum amount of metabolic energy necessary to move 1 g of crab 1 km. The average aerobic cost per distance for the 2-min E/2-min P protocol was significantly greater than the corresponding values for continuous exercise at the same AvS \((P < 0.05)\). The average aerobic cost per distance for other intermittent exercise protocols was not significantly different from the values corresponding to continuous exercise at the same AvS. At the highest AvS values tested \((0.23 \text{ and } 0.30 \text{ m/s})\), the aerobic cost per distance was not different from \( C_{\text{min}} \).

**Distance Capacity**

**Constant E-to-P ratio.** Crabs exercising intermittently when E was 2 min \((E/P = 1)\) traveled 5.8-fold farther than the same AvS \((0.30 \text{ m/s, a supramaximal speed; } P < 0.001)\) and 2.2-fold farther than those moving at the same AvS \((0.15 \text{ m/s, a submaximal speed; } P < 0.05; \text{ Fig. 4})\). When E was 3 min, the distance capacity was twofold greater than the same AvS 

**Distance Capacity**

**Constant E-to-P ratio.** Crabs exercising intermittently when E was 2 min \((E/P = 1)\) traveled 5.8-fold farther than those moving continuously at the same AvS \((0.23 \text{ and } 0.30 \text{ m/s, a supramaximal speed; } P < 0.001)\) and 2.2-fold farther than those moving at the same AvS \((0.15 \text{ m/s, a submaximal speed; } P < 0.05; \text{ Fig. 4})\). When E was 3 min, the distance capacity was twofold greater than the same AvS. When E was very short \((30 \text{ s})\) or very long \((4 \text{ or } 5 \text{ min})\) and P was equal to E, the distance capacity was not statistically different from the distance traveled continuously at the same AvS and was less than the total distance traveled before fatigue at the same AvS \((P < 0.05)\).

**Varied pause duration.** When E was 120 s, a 30-, 60-, and 120-s pause period significantly increased the distance capacity compared with continuous exercise at the same AvS \((P < 0.05)\) and the same AvS \((P < 0.05; \text{ Table 2})\). The longest pause duration \((i.e., 120 \text{ s})\) resulted in the greatest distance capacity.

When E was 30 s, an increase in P did not increase distance capacity \((Table 2)\). The total distance traveled intermittently was not significantly different from the distance traveled continuously at the same AvS when P was 5 and 15 s and was significantly less than the distance traveled continuously at the same AvS when P was 30 and 60 s \((P < 0.05)\).

**Varied speed.** When the speed of the exercise interval was increased from 170 \((0.30 \text{ m/s})\) to \(220\% \text{ MAS} \(0.40 \text{ m/s})\), the distance capacity decreased significantly \((P < 0.03)\). The distance capacity for intermittent exercise in which the speed of the exercise period was \(0.30 \text{ m/s (E = 5 s and P = 10 s)}\) was not significantly different from the distance traveled continuously at the same AvS but was significantly less than the total distance traveled before fatigue for crabs exercising continuously at the same AvS \((P < 0.05; \text{ Table 3})\). At the speed of \(0.40 \text{ m/s (E = 6 s and P = 12 s)}\) the distance capacity was significantly greater than the total distance traveled continuously at the same AvS \((P < 0.05)\) but was significantly less than the distance capacity for crabs exercising continuously at the same AvS \((P < 0.05)\).

**Leg Muscle Lactate**

Resting levels of lactate were \(1.3 \pm 0.1 \mu M/g\) leg \((Table 4)\). Crabs that exercised continuously at \(0.30 \text{ m/s} \text{ after } 7.5 \pm 0.9 \text{ min (n = 6)}\) Crabs in all exercise groups had significantly higher lactate levels than resting crabs \((P < 0.05)\). No significant differences were found between the CE and IE groups or between the CE and IP groups. However, the lactate concentration in the IP group was significantly lower than that in the IE group \((P < 0.05)\). In the IE group, the lactate levels were higher in the trailing leg than in the leading leg \((P < 0.01)\).

**DISCUSSION**

**Distance Capacity**

**Intermittent vs. continuous exercise.** The limited aerobic capacities of ectotherms, relative to endotherms, per-

**Table 2. Effect of pause duration on distance capacity**

<table>
<thead>
<tr>
<th>Exercise Period, s</th>
<th>Pause Period, s</th>
<th>Distance Capacity, m</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Intermittent exercise</td>
</tr>
<tr>
<td>120</td>
<td>30</td>
<td>304.8±61.0**†</td>
</tr>
<tr>
<td>120</td>
<td>60</td>
<td>215.4±62.4**†</td>
</tr>
<tr>
<td>120</td>
<td>120</td>
<td>798.7±142.8**†</td>
</tr>
<tr>
<td>30</td>
<td>5</td>
<td>206.8±74.6</td>
</tr>
<tr>
<td>30</td>
<td>15</td>
<td>129.8±23.3</td>
</tr>
<tr>
<td>30</td>
<td>30</td>
<td>105.3±20.8**†</td>
</tr>
<tr>
<td>30</td>
<td>60</td>
<td>125.6±36.3†</td>
</tr>
</tbody>
</table>

Values are means ± SE; n = 5 for each intermittent exercise protocol. Values for distance capacity for continuous exercise at same AvS are estimated from data reported by Full \((21)\). * Significantly different from distance capacity at same AvS \((P < 0.05)\); † Significantly different from distance capacity at same AvS \((P < 0.05)\).
mit only certain types of low-intensity continuous behaviors and preclude others that are of high intensity and demand stamina. The extent of these limitations has, thus far, only been determined for constant-speed steady-state exercise. The present results show that dynamic non-steady-state physiological adjustments can alter behavioral capacity and must be considered in ectotherms. Behaving intermittently can significantly alter the limitations on endurance determined during continuous activity.

The aerobic capacity of most ectotherms is an order of magnitude less than that of endotherms (6, 20, 24, 56). The highly active ghost crab is no exception (21). Because \( \dot{V}O_2 \) increases linearly with speed in most pedestrians, the low \( \dot{V}O_2 \) of ectotherms is attained at speeds 1/7–1/10 that of endotherms (29). Ghost crabs change gait from a walk to a trot and a trot to a gallop at speeds similar to that of a mammal of the same body mass (22, 27). However, ghost crabs attain MAS at a slow walking speed, whereas a quadrupedal mammal can gallop before exceeding \( \dot{V}O_2 \) max (34). The speed at which \( \dot{V}O_2 \) max is attained is correlated with an inability to sustain continuous locomotion. Endurance of continuous steady-state exercise in the ghost crab decreases significantly at speeds approaching MAS (i.e., 0.18 m/s; Fig. 5).

Exercising intermittently can increase the distance capacity of ghost crabs significantly compared with continuous exercise and at the same time can permit behaviors of high intensity (i.e., supramaximal). With particular exercise and pause durations, crabs can walk further intermittently than they do continuously when compared at the same AbS or at the same AvS (Fig. 5). Not surprisingly, ghost crabs exercising intermittently (at 0.3 m/s; \( E = 2 \) min, \( P = 2 \) min) could walk 5.8-fold farther before fatigue than they could by exercising continuously at the same AbS. More importantly, however, a ghost crab could also walk twice as far intermittently at the same AvS used during continuous exercise (0.15 m/s) by walking twice as fast and resting half the time (Fig. 5). A ghost crab walking at speeds eliciting \( \dot{V}O_2 \) max (0.30 m/s) and resting half the time could still travel twice as far as a crab walking continuously at a speed that did not exceed \( \dot{V}O_2 \) max (0.15 m/s). By exercising intermittently ghost crabs were able to attain distance capacities more comparable to an animal walking continuously with a greater \( \dot{V}O_2 \) max and MAS. A speed that may demand 84% \( \dot{V}O_2 \) max when traveled continuously may only demand 73% if the crab moves intermittently.

Distance capacity is not increased simply by moving intermittently. The present results show that it may be reduced significantly relative to continuous exercise (Fig. 5). When ghost crabs alternate 30 s of exercise at 0.30 m/s with 30-s pause periods, distance capacity was decreased 3.4-fold compared with crabs exercising at the same AvS (0.15 m/s; Fig. 4 and Table 2). This example illustrates that behavior can be constrained if animals are forced to be active intermittently.

**Effect of exercise and pause durations.** Distance capacity of intermittent activity in ghost crabs is highly dependent on both the exercise and pause durations (Fig. 4 and Table 2). Studies of intermittent exercise on humans show that supramaximal exercise can be sustained if the exercise period is <30 s and the pause period is at least twice as long as the exercise period (19, 52). By contrast, the ghost crab fatigued quickly even when the duration of the pause period (e.g., 60 s) was twice that of the exercise period (e.g., 30 s). Using this protocol, crabs walked no further than during continuous exercise at the same AbS (Table 2). In general, longer durations of pause (i.e., >60 s) and exercise (i.e., >30 s) periods resulted in the greatest distance capacity of ghost crabs.

A pause of <30 s may be too short for ghost crabs to recover from the preceding exercise period before beginning the next exercise period (Fig. 4 and Table 2). The critical pause duration in ghost crabs appears to be between 30 and 120 s. When the pause periods were =30 s and the exercise period was 120 s, the total distance traveled by ghost crabs before fatigue was greater for intermittent exercise than for continuous exercise at the same AbS and AvS (Fig. 5 and Table 2). The longest pause duration (i.e., 120 s) resulted in a threefold increase in distance capacity compared with a pause duration of 60 s. Pause periods of <30 s did not result in distance
27. Full, R. J., and R. B. Weinstein. Integrating the physiology, mechanics, and behavior of rapid running ghost crabs: slow and steady doesn't always win the race. Am. Zool. in press.