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Thermal Dependence of Locomotor Energetics and Endurance Capacity in the Ghost Crab, *Ocypode quadrata*

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Abstract

We tested a general model predicting the effect of body temperature (T_b) on the aerobic capacity, metabolic cost, and endurance of sustained, terrestrial locomotion. In the ghost crab, *Ocypode quadrata*, T_b was a function of ambient temperature (T_a), relative humidity (RH), and the duration of acute exposure. At 15°C and 24°C, T_b was similar to T_a . At high T_a (30°C to 35°C) and low RH (40% to 50%), T_b 's were 6°C below T_a . When the RH was 99%–100% at a T_a of 30°C, T_b stabilized at 29.7°C. The depression in T_b resulted from evaporative water loss. The maximal rate of oxygen consumption ($\dot{V}O_{2\max}$), determined during treadmill exercise, decreased by nearly 75% as T_b was decreased from 24°C to 15°C. The minimum cost of locomotion (C_{\min} , the slope of the steady state oxygen consumption vs. speed function) did not change at low T_b (15°C). As T_b was increased from 24°C to 30°C, $\dot{V}O_{2\max}$ decreased to half of its original value. At the lowest walking speeds, steady state oxygen consumption ($\dot{V}O_{2ss}$) at a T_b of 30°C did not differ significantly from or may have even exceeded that at a T_b of 24°C (the y-intercept of the $\dot{V}O_{2ss}$ vs. speed function was elevated relative to resting rates). The minimum cost of locomotion decreased by nearly two-thirds when T_b was raised from 24°C to 30°C. The reduced C_{\min} increased the range of sustainable speeds by nearly threefold over that predicted from a thermally insensitive C_{\min} at a T_b of 30°C. Endurance correlated with the speed at which $\dot{V}O_{2\max}$ was attained (maximum aerobic speed) and, therefore, was reduced significantly at both low and high temperatures. On the basis of the present study of quantified locomotion, we conclude that thermal optima of maximal oxygen consumption and endurance are caused by a true thermal effect on oxygen utilization and muscle function rather than by a submaximal effort by the animal.

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Introduction

A general ectothermic model of the effect of temperature on aerobic capacity, endurance, and the metabolic cost of locomotion has emerged over the last 20 yr (Herreid, Full, and Prawel 1981*a*; John-Alder and Bennett 1981; Full et al. 1988; Gatten, Miller, and Full 1992). Body temperature (T_b) is assumed to be equal to ambient temperature (T_a) in controlled laboratory performance tests. Most rate processes in these tests show a typical thermal dependence. Rates of maximal oxygen consumption ($\dot{V}_{O_{2\max}}$), resting oxygen consumption ($\dot{V}_{O_{2\text{rest}}}$), oxygen consumption at the slowest speeds (y-intercept of the \dot{V}_{O_2} vs. speed function), as well as rates of locomotion at which $\dot{V}_{O_{2\max}}$ is attained (maximum aerobic speed [MAS]), nearly double or triple with a 10°C increase in temperature ($Q_{10} = 2-3$). A greater MAS results in a greater range of sustainable speeds. The thermal dependence of submaximal oxygen consumption rates at a given speed decreases as speed is increased (i.e., Q_{10} decreases with speed). The result is a thermal shift in \dot{V}_{O_2} at the slowest speeds (i.e., a thermally sensitive y-intercept of the \dot{V}_{O_2} vs. speed function) but no thermal alteration in the linear increase in oxygen consumption with increased speed (i.e., a thermally insensitive slope). The increase of oxygen consumption with speed, termed the minimum cost of locomotion (C_{\min} ; Taylor, Schmidt-Nielsen, and Raab 1970), has been found to be relatively temperature-independent in a wide variety of species (Herreid et al. 1981*a*; John-Alder and Bennett 1981; Bennett and John-Alder 1984; Houlihan and Innes 1984; Lighton and Feener 1989; Full and Tullis 1990).

In studies of general ectothermic activity (i.e., tumbling, prodding, or electric shock), aerobic capacity increases with temperature to a maximum (McFarland and Pickens 1965; Rutledge and Pritchard 1981; Bennett 1982; Gatten et al. 1992). The highest temperatures result in no further increase or even in a decline in peak oxygen consumption. Measurements during quantified, steady state locomotion in the death-head cockroach, *Blaberus discoidalis*, confirm that at the highest temperatures $\dot{V}_{O_{2\max}}$ does not increase with an increase in temperature (Full and Tullis 1990). Because speed was controlled, the possibility that the lack of increase in \dot{V}_{O_2} at the highest temperatures simply results from a submaximal output is rejected. The cockroach's endurance at the highest temperatures is correlated with the MAS and remains the same or decreases despite an 11°C increase in ambient temperature. Full and Tullis (1990) also discovered that T_b does not always equal T_a , even under controlled thermal conditions in the laboratory. Death-head cockroaches increase T_b up to 6°C as they run. The temperature increase is not curtailed at the highest T_a , so that the limitation in aerobic

capacity and endurance actually occurs at a T_b nearer the upper lethal limit ($\sim 42^\circ\text{C}$).

In this study and its companion (Weinstein, Full, and Ahn 1994), we test the general model relating aerobic capacity to endurance and the metabolic cost of locomotion on the ghost crab, *Ocypode quadrata*. We selected this species because our preliminary measurements suggested its study may lead to further development of the general model. We discovered that, as in the death-head cockroach, T_a does not equal the ghost crab's T_b at high temperatures (i.e., at 30°C). Body temperature can be depressed by 6°C below ambient temperature. This finding led us to hypothesize that, if T_b were forced to increase, then ghost crabs may be the first species to show a marked decrement in performance during quantified terrestrial locomotion. Moreover, since evaporation of water appeared to be the only mechanism for cooling, we questioned what the effect of water loss may be on the relationships among aerobic capacity, endurance, and the metabolic cost of locomotion (Weinstein et al. 1994).

Material and Methods

Animals

Ghost crabs, *Ocypode quadrata*, (mass, $29.2 \text{ g} \pm 9.2 \text{ g}$ [mean ± 1 SD]; $n = 48$) were collected from the beaches surrounding the Duke University Marine Laboratory in Beaufort, North Carolina. In this location, ghost crabs are primarily active above ground from late May through October and spend the winter months underground (Wolcott 1978). This population is largely nocturnally active, emerging from burrows after dusk and moving and foraging actively until dawn. Some individuals migrate as far as 300 m along the beach in one night (Wolcott 1978). Body temperatures of nocturnally active crabs in the summer range from 17° to 28°C (air temperature range = 19° – 28°C , relative humidity [RH] range = 57%–95%; R. B. Weinstein, unpublished data). Ghost crabs are rarely active at ambient temperatures less than 15° – 20°C , even though their body temperatures are likely to be well above their lower lethal limit (6° – 8°C ; T. Wolcott, personal communication).

Animals were transported overnight by air to our laboratory in Berkeley, California. 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 a 14L:10D photoperiod at 24°C and 75% RH. The crabs were fed fresh fish three to four times a week and their containers were filled with fresh seawater 24 h after feeding. Only intermolt crabs were used. Individuals rested for at least 4 d between trials.

Body Temperature

Body Temperature Measurements. Body temperature was measured with a thermocouple (copper (+)/ constantan (-) Teflon leads, 0.02 mm diameter). The thermocouple leads were connected to a microprocessor thermometer (Model HH23, Type K connector, Omega) and were calibrated from 0°C to 40°C. Crabs were placed in a cold room (4°C) for 15 min prior to insertion of the thermocouple. A small hole (1 mm) was made in the ventral carapace surface. The thermocouple tip was threaded through the opening to a depth of approximately 5 mm within the levator muscle adjacent to the third walking leg. The thermocouple leads were fastened to the crab's dorsal carapace surface with a small amount of liquid adhesive (cyanoacrylate). After placement of the thermocouple, crabs were returned to the environmental chamber (24°C) and provided with access to 30%–50% sea-water for at least 3 h before further experimentation.

Body Temperature during Rest. Ghost crabs rested in a miniature treadmill-respirometer. The respirometer was placed inside an incubator (Fisher Low Temperature Incubator, Model 146) to control T_a at 15°, 24°, 30°, or 35°C. At a T_a of 30°C, live crabs were exposed to either normal room air (40%–50% RH) or humidified air (99%–100% RH). The rate of airflow (FR) was 200 mL min⁻¹ at T_a 's of 15°C and 30°C (40%–50% RH) and 300 mL min⁻¹ at T_a 's of 24°, 30° (99%–100% RH), and 35°C. Body temperature was recorded at 5-min intervals for 60 min.

Body Temperature during Exercise. Crabs were placed in the treadmill chamber at a T_a of either 30°C or 35°C with 40%–50% RH for 1 h prior to exercise. At a T_a of 30°C, crabs exercised for 10 min at 0.36 km h⁻¹ or 0.72 km h⁻¹ for 2 min. At a T_a of 35°C, crabs exercised for 5 min at 0.36 km h⁻¹. Measurements of T_b were taken at 30-s or 60-s intervals for the entire exercise period.

Aerobic Metabolism

Oxygen Consumption Measurements. Crabs were exercised in a miniature treadmill-respirometer. The relative humidity of the air leaving the chamber was measured (Digital Hygrometer, Fisher Scientific), and water vapor was subsequently removed with Drierite. Carbon dioxide was removed with Ascarite. The flow rate was 200 mL min⁻¹ or 300 mL min⁻¹, depending on the experimental protocol. The oxygen concentration was monitored with an O₂ analyzer (S3A, Ametek) interfaced with a personal computer (Macintosh II) and data acquisition hardware (NB MIO-16, National Instruments) and software (LabView, National Instruments). The mass-specific, steady

state rate of oxygen consumption ($\dot{V}_{O_{2ss}}$) was calculated from the O_2 concentration (Withers 1977). Calculations of instantaneous \dot{V}_{O_2} (Herreid, Prawel, and Full 1981*b*; Full 1987) were not significantly different from standard calculations. The treadmill-respirometer was placed in an incubator (Fisher Low Temperature Incubator, Model 146) to control ambient temperature at 15°, 24°, or 30°C.

Resting Metabolic Rate, Steady State Oxygen Consumption, and Maximal Rate of Oxygen Consumption. Animals were placed in the treadmill chamber for 60 min to allow thermal equilibration prior to data collection. Measurements of $\dot{V}_{O_{2\text{rest}}}$ were taken for 10 min while the crabs rested quietly. Maximal oxygen consumption was determined by a multiple-speed, progressive maximal test (Full and Herreid 1983). After the 10-min rest period, crabs were exercised at an intermediate speed. On attaining a steady state oxygen consumption for 3 min, the speed of the treadmill belt was increased to a greater speed until a new higher steady state was attained. Three minutes after the new steady state had been reached, speed was increased again. The maximum rate of oxygen consumption was defined as the rate of oxygen consumption (\dot{V}_{O_2}) attained when two consecutive incremental increases in speed resulted in no further increase in \dot{V}_{O_2} . The steady state rate of oxygen consumption measured during the multiple-speed progressive test provided values similar to the \dot{V}_{O_2} determined during single-speed tests.

Effect of Body Temperature. To determine the effect of T_b on metabolic rate, crabs were exercised at three body temperatures (15°, 24°, or 30°C). To achieve a T_b of 15°C, crabs rested in the treadmill chamber for 60 min at a T_a of 15°C prior to data collection to allow for thermal equilibration. The airflow rate was 300 mL min⁻¹ and the RH in the treadmill chamber was 40%–50%. To reach a T_b of 30°C, crabs rested in the treadmill chamber at a T_a of 30°C and an RH of 99%–100% (FR of 300 mL min⁻¹) for 60 min prior to data collection. Data for crabs exercising at a T_b of 24°C (FR = 300 mL min⁻¹; 40%–50% RH; 30-min rest period) are from Full (1987). Several individuals from the present group of animals were tested to ensure consistency with prior data. Since the energetic and endurance measurements of these individuals were similar to the previously published values, we felt it unnecessary to repeat the entire data set.

Endurance Capacity

After 1 h of thermal equilibration in the treadmill chamber, crabs were exercised to fatigue at a selected speed. To test the effect of T_b , endurance capacity (T_{end}) was compared for crabs exercising at T_b 's of 15°, 24°, and

30°C. Speeds ranged from 0.14 km h⁻¹ to 0.72 km h⁻¹ at 15°C and 0.28 km h⁻¹ to 0.79 km h⁻¹ at 30°C. Data for crabs exercising at 24°C are from Full (1987). The 24°C data were replicated in the present group of animals. Crabs maintained a consistent pace without prodding until just before fatigue. An animal was considered fatigued when it failed to keep pace with the treadmill belt, dragged its abdomen, or did not respond to three successive prodding attempts. The trial was halted if endurance time exceeded 2 h. Trials during which crabs walked erratically or struggled were aborted.

Results

Body Temperature

Body Temperature during Rest. The initial T_b of ghost crabs acclimated at 24°C was $24.1^\circ \pm 0.2^\circ\text{C}$ (mean \pm 1 SE; $n = 30$). At T_a 's of 15°C and 24°C, T_b was similar to T_a . When crabs were exposed to a T_a of 15°C, T_b decreased and stabilized near 15°C within 45–50 min (fig. 1). The half-time required to reach the steady state T_b was 14.2 min. After 60 min, T_b was $15.6^\circ \pm 0.5^\circ\text{C}$ ($n = 6$; figs. 1 and 2). For crabs placed in the chamber at a T_a of 24°C, T_b

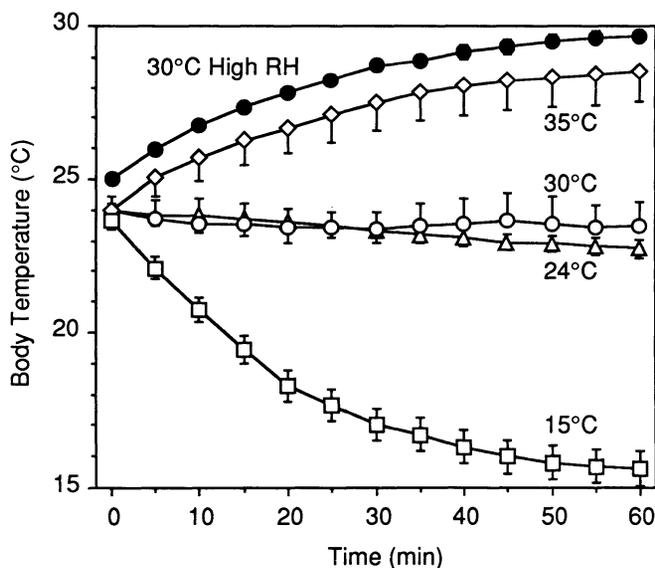


Fig. 1. Body temperature of resting ghost crabs. Body temperature during 1 h of thermal equilibration at 40%–50% RH and T_a 's of 15°C (squares), 24°C (triangles), 30°C (open circles), and 35°C (diamonds) after transfer from a 24°C environment. Closed circles represent T_b 's of crabs exposed to 99%–100% RH and a T_a of 30°C. Error bars represent 1 SE.

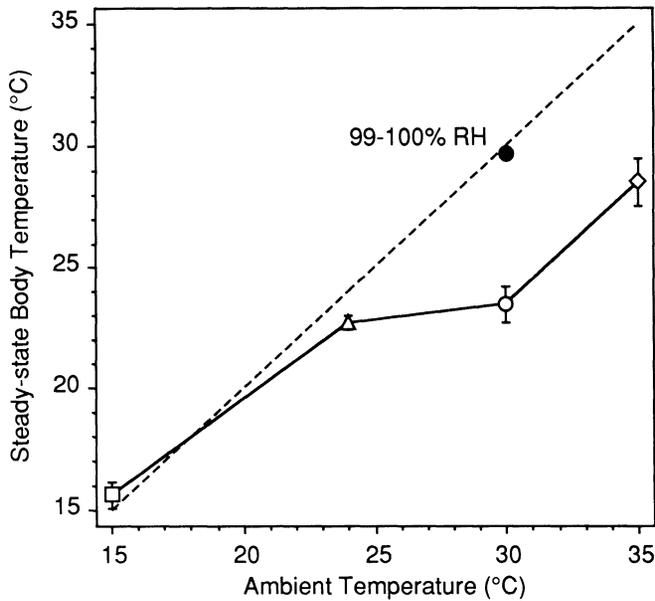


Fig. 2. Body temperature as a function of T_a after 60 min of thermal equilibration. Symbols are as in figure 1. Error bars represent 1 SE. The dashed line represents $T_b = T_a$.

remained near 24°C for the entire experimental period (fig. 1). After 60 min, T_b was $22.7 \pm 0.3^\circ\text{C}$ ($n = 6$; fig. 2). At higher temperatures ($T_a = 30^\circ\text{C}$ and 35°C) with low RH, T_b did not reach T_a . Instead, after 60 min at a T_a of 30°C , T_b remained near room temperature ($23.5 \pm 0.8^\circ\text{C}$; $n = 6$; fig. 1), which was approximately 6°C below T_a (fig. 2). At a T_a of 35°C , T_b increased and stabilized near $28.5 \pm 1.0^\circ\text{C}$ ($n = 6$; fig. 1), which was also approximately 6°C below T_a (fig. 2). The half-time required to reach the steady state T_b was 15.0 min.

The highest T_b we measured was for crabs exposed to humidified air at a T_a of 30°C . For these crabs, T_b leveled off near 30°C within 45–50 min (fig. 1). The half-time required to reach the steady state T_b was 14.7 min. At the end of the 60-min rest period, T_b was $29.7 \pm 0.2^\circ\text{C}$ ($n = 6$; fig. 2).

Body Temperature during Exercise. At each period, the change in body temperature from the initial T_b at the start of exercise was calculated for each individual and plotted as a function of time. Body temperatures at the beginning of the exercise period were approximately 6°C below the ambient temperatures. During exercise, the crabs experienced little change in T_b . At a T_a of 30°C , T_b dropped by 0.2°C during the first 30–120 s and then increased slightly throughout the remainder of the exercise period. An initial drop in T_b was not seen at a T_a of 35°C . The largest change in T_b was exhibited

by crabs exercising at 0.36 km h^{-1} at a T_a of 30°C . However, this change was less than 0.5°C at the end of the 10-min exercise period. In other words, a crab with a T_b of 23.5°C after a 60-min rest period at a T_a of 30°C (40%–50% RH) had a T_b of 23.9°C after 10 min of exercise.

Aerobic Metabolism

Resting Oxygen Consumption. The rate of oxygen consumption during the 10-min rest prior to exercise was averaged to obtain $\dot{V}O_{2 \text{ rest}}$. Mass-specific $\dot{V}O_{2 \text{ rest}}$ increased over the 15°C – 24°C body temperature range. Crabs resting at 15°C ($n = 5$) had a significantly lower $\dot{V}O_{2 \text{ rest}}$ than those at 24°C ($n = 7$; Mann-Whitney U -test, $P < 0.05$) or 30°C ($n = 5$; Mann-Whitney U -test, $P < 0.05$; figs. 3, 4). The rate of oxygen consumption during the rest period was not significantly different for crabs with T_b 's of 24°C and 30°C (Mann-Whitney U -test, $P > 0.05$).

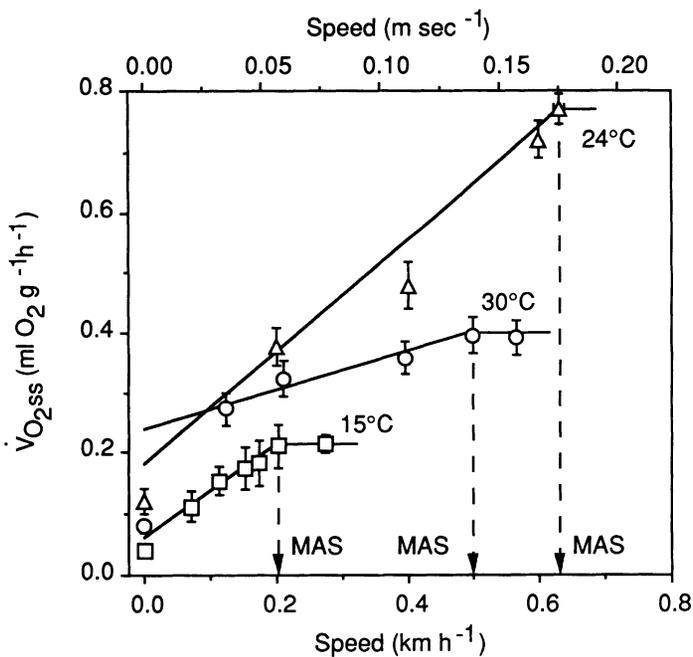


Fig. 3. Steady state oxygen consumption and $\dot{V}O_{2 \text{ max}}$ as a function of speed at T_b 's of 15°C (squares; $n = 5$), 24°C (triangles; $n = 5$), and 30°C (circles; $n = 7$). Resting rates are shown at zero speed. The slope of the $\dot{V}O_{2 \text{ ss}}$ vs. speed function is the C_{min} . Error bars represent 1 SE. Dashed arrows show the MAS. The data for 24°C are taken from Full (1987), where $\dot{V}O_{2 \text{ max}}$ and MAS were determined by a step test with small incremental increases in speed.

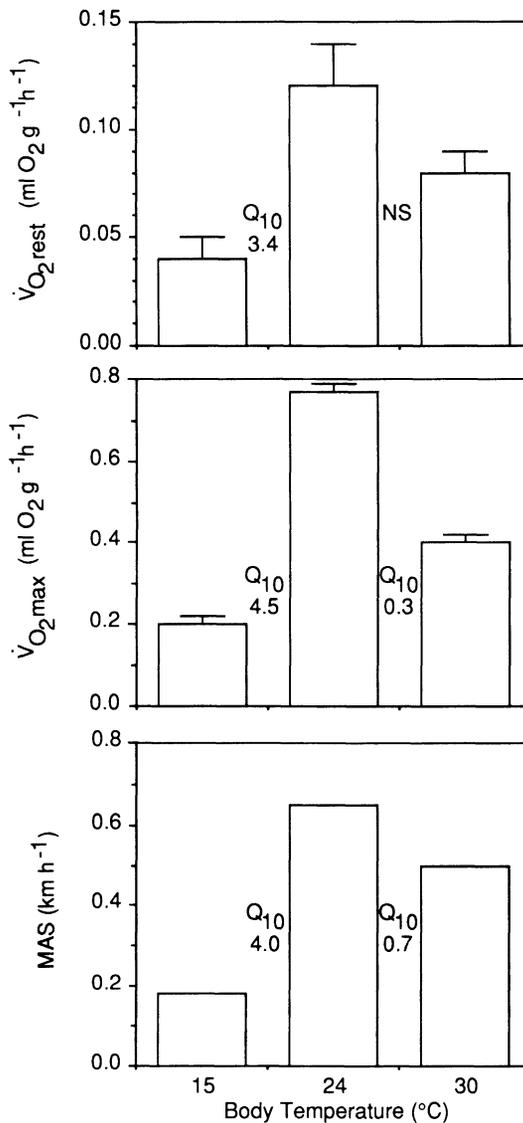


Fig. 4. Resting rate of oxygen consumption, $\dot{V}O_{2\text{max}}$, and MAS as a function of T_b . Thermal dependence is indicated for the 15°–24° C and 24°–30° C ranges. Error bars represent 1 SE. The resting rate of oxygen consumption did not change significantly (NS) when T_b increased from 24° to 30° C. The resting rate of oxygen consumption, $\dot{V}O_{2\text{max}}$, and MAS were greatest at 24° C.

Steady State Oxygen Consumption versus Speed and the Minimum Cost of Locomotion. The steady state rate of oxygen consumption was calculated by averaging the $\dot{V}O_2$ for the last 3 min of exercise at each speed. The steady state rate of oxygen consumption increased linearly with speed at all three

TABLE 1
Aerobic metabolism and minimum cost of locomotion of Ocypode quadrata at 15°, 24°, and 30°C

T_b	$\dot{V}O_{2\max}/\dot{V}O_{2\text{rest}}$	$\dot{V}O_{2\text{ss}}$ (mL O ₂ g ⁻¹ h ⁻¹) versus Speed (km h ⁻¹)	y-Intercept/ $\dot{V}O_{2\text{rest}}$
15°C ...	5.0	.76 (± .35) v + .06 ^a	1.5
24°C ...	6.4	.86 (± .13) v + .18 ^b	1.5
30°C ...	5.0	.31 (± .20) v + .24 ^c	3.0

Note. Body temperature is T_b . The resting rate of oxygen consumption is $\dot{V}O_{2\text{rest}}$; the maximal rate of oxygen consumption is $\dot{V}O_{2\max}$; the steady state oxygen consumption is $\dot{V}O_{2\text{ss}}$; and v is speed. One standard error of the slope for the $\dot{V}O_{2\text{ss}}$ vs. speed regression equation is indicated in parentheses. The slope of the regression equation is the minimum cost of locomotion (mL O₂ g⁻¹ km⁻¹). Values for $T_b = 24^\circ\text{C}$ are from Full (1987).

^a $r^2 = 0.21$; $P = 0.04$.

^b $r^2 = 0.78$; $P < 0.001$.

^c $r^2 = 0.20$; $P = 0.04$.

T_b 's (fig. 3). The slope of the $\dot{V}O_{2\text{ss}}$ versus speed function is equal to C_{\min} , which represents the minimum amount of metabolic energy necessary to move 1 g of crab 1 km (Taylor et al. 1970). The minimum cost of locomotion was not significantly different for crabs with a T_b of 15°C and 24°C (model, $\dot{V}O_2 = \text{constant} + \text{temperature} + \text{speed} + \text{temperature} \times \text{speed}$; $F_{(1,31)} = 0.4$, $P > 0.05$; table 1). However, C_{\min} was significantly lower for crabs with a T_b of 30°C than for crabs with T_b 's of either 15°C or 24°C ($F_{(1,32)} = 15.2$, $P < 0.01$; fig. 3; table 1). The y-intercept value was temperature sensitive. The y-intercept was lower at a T_b of 15°C than it was at a T_b of 24°C (ANCOVA model, $\dot{V}O_2 = \text{constant} + \text{temperature} + \text{speed}$; $F_{(1,31)} = 14.1$, $P < 0.01$) and was higher at a T_b of 30°C than at a T_b of 24°C ($F_{(1,32)} = 11.0$, $P < 0.01$; fig. 3; table 1). At each T_b , the y-intercept value was elevated above the resting metabolic rate (table 1).

Maximal Rate of Oxygen Consumption. Mass-specific $\dot{V}O_{2\max}$ was strongly affected by T_b . The maximum rate of oxygen consumption was higher at a T_b of 24°C than at a T_b of 15°C (Mann-Whitney U -test, $P < 0.05$) or of 30°C (Mann-Whitney U -test, $P < 0.05$; figs. 3, 4). The maximum rate of oxygen consumption was higher at a T_b of 30°C than at a T_b of 15°C (Mann-Whitney U -test, $P < 0.05$). The thermal dependence of $\dot{V}O_{2\max}$ was greater over the 15°–24°C range than it was over the 24°–30°C range (fig. 4). The aerobic

factorial scope ($\dot{V}O_{2\text{ max}}/\dot{V}O_{2\text{ rest}}$), indicating the capacity to increase the rate of oxygen above the resting rate, was greatest at 24°C (fig. 4).

Metabolic Cost of Locomotion. The total metabolic cost of locomotion (C_{tot} , where $C_{\text{tot}} = \dot{V}O_{2\text{ ss}}/\text{speed}$) for the ghost crab was dependent on speed and body temperature (fig. 5). At all body temperatures, C_{tot} decreased with an increase in speed, because $\dot{V}O_{2\text{ rest}}$ and the y-intercept became a smaller percentage of the total cost at the higher speeds. Crabs exercising at a T_b of 24°C had a higher rate of oxygen consumption than crabs exercising at a T_b of 30°C at all except the slowest speeds. The high $\dot{V}O_{2\text{ ss}}$ at 24°C increased the total metabolic energy required to travel a given distance. Crabs at a T_b of 15°C had the lowest $\dot{V}O_{2\text{ rest}}$ and $\dot{V}O_{2\text{ ss}}$ and, therefore, had the lowest total cost of locomotion at any given speed (fig. 5).

Maximum Aerobic Speed. The slowest speed that elicits $\dot{V}O_{2\text{ max}}$ is the MAS (John-Alder and Bennett 1981). At T_b 's of 15°C and 30°C, the values for $\dot{V}O_{2\text{ ss}}$ at the fastest two speeds tested were not significantly different from one another (Mann-Whitney *U*-test, $P > 0.05$). Therefore, on the basis of

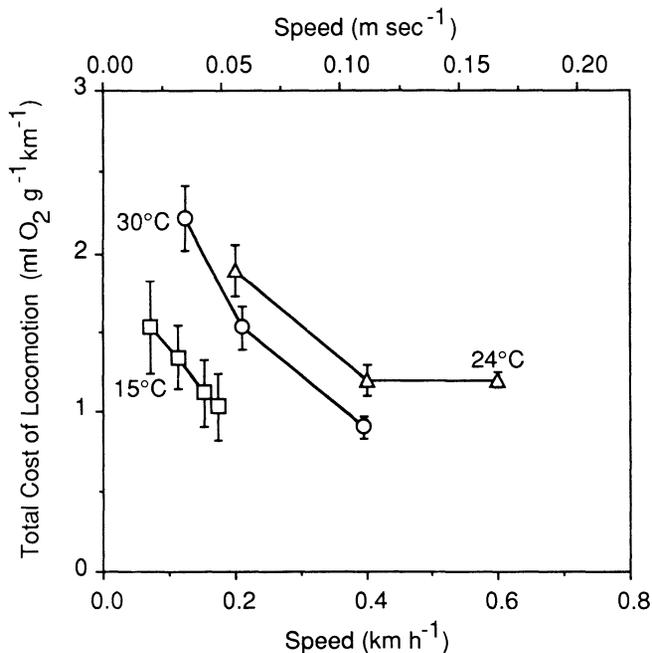


Fig. 5. Total cost of locomotion as a function of speed at T_b 's of 15°C (squares; $n = 5$), 24°C (triangles; $n = 5$), and 30°C (circles; $n = 7$). The total cost of locomotion decreased with an increase in speed at all body temperatures. Crabs with a body temperature of 15°C had the lowest C_{tot} . Error bars represent 1 SE.

the regression through the submaximal $\dot{V}O_{2ss}$ and the value for $\dot{V}O_{2max}$, the second fastest speed at 15°C and at 30°C was considered the MAS. Crabs exercising at a T_b of 15°C attained $\dot{V}O_{2max}$ at the slowest speed and, therefore, had the lowest MAS (figs. 3, 4). Crabs exercising at a T_b of 24°C had the greatest MAS. The thermal dependence of the MAS was greater over the 15°–24°C range than over the 24°–30°C range (fig. 4).

Endurance

Endurance capacity (time to fatigue) decreased exponentially as exercise speed increased at each ambient temperature tested (fig. 6) and was strongly influenced by temperature. At 24°C, crabs showed the greatest endurance capacity over the range of speeds tested ($n = 16$; $T_{end} = 0.027v^{-4.66}$, where T_{end} is measured in hours and speed [v] in km h^{-1} ; $r^2 = 0.84$; fig. 6). Crabs exercised at 15°C ($n = 18$; $T_{end} = 0.021v^{-1.51}$; $r^2 = 0.86$) had a significantly lower endurance capacity compared to crabs with a T_b of 24°C (ANCOVA model for log-transformed data, endurance = constant + temperature + speed; $F_{(1,28)} = 7.0$, $P = 0.01$). Crabs exercised at a body temperature of

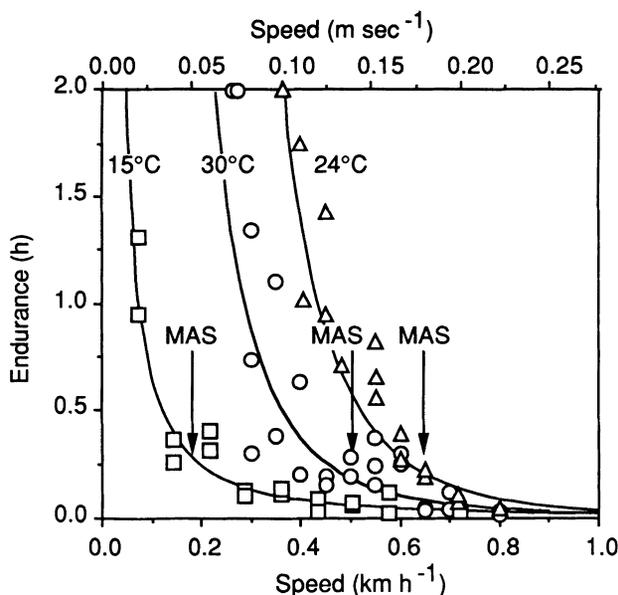


Fig. 6. Endurance time as a function of speed at T_b 's of 15°C (squares; $n = 18$), 24°C (triangles; $n = 17$), and 30°C (circles; $n = 24$). Endurance capacity was correlated with MAS (see fig. 4; experiments were terminated after 2 h if the crab had not yet become fatigued. These data are shown on the graph but were not used for calculation of the endurance equation).

30°C had an intermediate capacity ($n = 22$; $T_{\text{end}} = 0.023v^{-3.02}$; $r^2 = 0.69$) compared to those with T_b 's of 15°C and 24°C (fig. 6). Crabs exercised at 24°C attained $\dot{V}_{O_2 \text{ max}}$ at a faster speed than crabs exercising at 15°C and 30°C (fig. 3), which indicates that the differences in endurance are correlated with the differences measured for the MAS.

Discussion

Body Temperature

In the search for the performance limits relating aerobic capacity to endurance and the metabolic cost of locomotion, T_b cannot be assumed to be equal to T_a . Although well established in field studies, the mismatch in T_b and T_a has not always been rigorously considered under controlled laboratory conditions. In the present study, the T_b of resting and active ghost crabs was dependent on T_a , the duration of exposure to a change in T_a , and RH. We measured a 6°C depression in the ghost crab's body temperature during rest and exercise at 30°C and 35°C when RH was low (figs. 1 and 2). The body temperature of fiddler crabs (*Uca* spp.) can be 2°–6°C below T_a when the crab is exposed to 25% RH (Edney 1961). More modest T_b depressions below T_a have been shown in other semiterrestrial crabs, such as *Carcinus maenus* and *Portunus marmoreus* (Ahsanullah and Newell 1977). After 60 min of exposure to air at a T_a of 21°C and 68% RH in the laboratory, the T_b 's of these crabs were 18°C and 19°C, respectively. The depression of T_b in ghost crabs followed a characteristic time course. After acute exposure to a change in T_a , stable T_b 's were attained within 60 min, and half-times to steady state T_b were approximately 15 min (fig. 1). These half-times are comparable to those reported for fiddler crabs (*Uca* spp.; Edney 1961) and two other semiterrestrial crabs (Ahsanullah and Newell 1977).

Evaporative water loss produced the depression of the ghost crab's T_b . This conclusion is supported by the lack of T_b depression in humidified air (figs. 1 and 2). Body temperature depression of other semiterrestrial crabs also decreases as the relative humidity increases (Ahsanullah and Newell 1977). The limitations on performance of this water loss are addressed in our companion study (Weinstein et al. 1994).

Oxygen Consumption

Body temperature elevation in ghost crabs exposed to 30°C under conditions that prevented evaporative cooling resulted in a 48% decrease in $\dot{V}_{O_2 \text{ max}}$ (figs. 3 and 4). The decrement in $\dot{V}_{O_2 \text{ max}}$ at 30°C was due to a thermal effect and not to submaximal effort. At the same workload (e.g., at 0.55 km h⁻¹),

the $\dot{V}_{O_{2ss}}$ at 30°C was approximately half the $\dot{V}_{O_{2ss}}$ at 24°C. Quantifying work rate or speed in the death-head cockroach showed that $\dot{V}_{O_{2max}}$ may plateau at high temperatures, but it did not demonstrate a significant decline in $\dot{V}_{O_{2max}}$ (Full and Tullis 1990). Both investigations lend necessary support to studies of uncontrolled activity that suggest a thermal optimum in peak \dot{V}_{O_2} (Halcrow and Boyd 1967; Bennett and Dawson 1972; Wilson 1974; Bennett, Dawson, and Bartholomew 1975; Rutledge and Pritchard 1981; Villarreal 1990).

Although studies of unquantified activity have shown a lack of increase in peak \dot{V}_{O_2} at the highest temperatures, few have shown the magnitude of deficit seen in ghost crabs (fig. 4). In the Australian crayfish, *Cherax tenuimanus*, the peak rate of oxygen consumption attains a plateau at high temperatures (>22°C) but not a significant decline (Villarreal 1990). The crayfish, *Pacifastacus leniusculus*, exhibits only a 16% decline in its peak rate of oxygen consumption with an increase in T_b at high temperatures (>20°C; Rutledge and Pritchard 1981). The decrement in peak \dot{V}_{O_2} in lizards ranges from 5% to 29% (Bennett and Dawson 1972; Wilson 1974).

The decline in the ghost crab's T_b from 24° to 15°C resulted in a predictable decrease in $\dot{V}_{O_{2max}}$ (fig. 4). The magnitude of the decrement was more surprising. The maximum rate of oxygen consumption at 15°C was only one-fourth the rate measured at 24°C, a $Q_{10(15^\circ-24^\circ C)}$ of 4.5. The thermal dependence of $\dot{V}_{O_{2max}}$ in the ghost crab over the 15°–24°C interval (fig. 4) is near the upper end of the range of values reported for peak or maximal \dot{V}_{O_2} in other crustaceans (Q_{10} range = 1.2–5.6; see, e.g., McFarland and Pickens 1965; Houlihan and Innes 1984; Villarreal 1990), in insects ($Q_{10(15^\circ-23^\circ C)}$ = 2.8; Full and Tullis 1990), and in lizards ($Q_{10(20^\circ-30^\circ C)}$ = 1.7–2.9; Bennett 1982).

The Minimum Cost of Locomotion, Maximum Aerobic Speed, and Endurance

The significant decrease in the ghost crab's $\dot{V}_{O_{2max}}$ at low and high T_b 's is in and of itself likely to contribute to a reduction in aerobically sustainable speeds. However, studies of controlled treadmill exercise demonstrate that endurance capacity is not determined by aerobic capacity alone (Full et al. 1988). Instead, the relationship between oxygen consumption and locomotor intensity (i.e., speed) must also be examined (Gatten et al. 1992). The speed at which $\dot{V}_{O_{2max}}$ is attained, the MAS (John-Alder and Bennett 1981), best correlates with endurance and is determined by the interaction of $\dot{V}_{O_{2max}}$ and C_{min} (Full et al. 1988). Economical locomotion (low C_{min}) can offset the reduction in the range of sustainable speeds associated with a low $\dot{V}_{O_{2max}}$. If cost increases less with an increase in speed, then $\dot{V}_{O_{2max}}$

will not be attained until higher speeds (i.e., higher MAS and greater range of sustainable speeds).

The decrease in $\dot{V}_{O_2 \max}$ in ghost crabs prevented from evaporative cooling at high T_a (30°C) did result in a marked decrease in MAS (fig. 4) and endurance (fig. 6). However, at the lowest walking speeds (<0.1 km h⁻¹), $\dot{V}_{O_{2ss}}$ at a T_b of 30°C did not differ significantly from or may even have exceeded that at a T_b of 24°C (i.e., the y-intercept of the $\dot{V}_{O_{2ss}}$ vs. speed function was elevated relative to resting rates; table 1). At higher speeds, $\dot{V}_{O_{2ss}}$ at a T_b of 30°C did not increase with speed to the same extent seen at 24°C and 15°C. The minimum cost of locomotion was decreased by two-thirds relative to the values at these lower temperatures. To our knowledge, this is the first demonstration that C_{\min} can be altered with a change in temperature. The elevated y-intercept at 30°C, coupled with the decrease in C_{\min} , makes a mechanistic explanation with respect to energy cost difficult. Although C_{\min} differs with temperature, the total cost of locomotion at the highest sustainable speeds varies little with T_b (fig. 5).

Nevertheless, the decrease in C_{\min} does have important consequences for ghost crabs with T_b 's equal to 30°C, because the reduction increases the MAS by 1.5–2.8-fold relative to what it would have been if C_{\min} had been equal to the value at T_b 's of 15°C and 24°C (fig. 3). In other words, if the C_{\min} had remained at 0.86 mL O₂ g⁻¹ km⁻¹ when T_b was raised to 30°C, the MAS (given the elevated y-intercept of 0.24 mL O₂ g⁻¹ h⁻¹ and a $\dot{V}_{O_2 \max}$ of 0.40 mL O₂ g⁻¹ h⁻¹) would have been 0.18 km h⁻¹ rather than 0.50 km h⁻¹. Similarly, if the C_{\min} had been 0.86 mL O₂ g⁻¹ km⁻¹ and the y-intercept had not been elevated (i.e., 1.5 times the $\dot{V}_{O_2 \text{rest}}$ at a T_b of 30°C, or 0.12 mL O₂ g⁻¹ h⁻¹), then the MAS (given a $\dot{V}_{O_2 \max}$ of 0.40 mL O₂ g⁻¹ h⁻¹) would have been only 0.33 km h⁻¹.

The limitation on the ghost crab's sustainable locomotor performance at 15°C was considerable (fig. 4). The large decline in $\dot{V}_{O_2 \max}$ was accompanied by a decrease in MAS ($Q_{10(15^\circ-24^\circ\text{C})} = 4$) and endurance (fig. 6). The minimum cost of locomotion was not altered when ghost crabs were cooled from 24°C to 15°C (fig. 3; table 1). The thermal independence of C_{\min} at these low temperatures was consistent with the general model developed from diverse species. The present results at low T_b may be explained mechanistically by the concept of recruitment compression (Rome, Loughna, and Goldspink 1984; Jayne, Bennett, and Lauder 1990). As T_b is decreased, ghost crabs may be forced to recruit more anaerobic fibers or muscles at lower speeds. The recruitment of less aerobic and more easily fatigued fibers or muscles at low temperatures may correlate with attaining $\dot{V}_{O_2 \max}$ at lower speeds, a greater reliance on anaerobic metabolism, and a reduction in endurance.

The extent of the decrease in sustainable performance at 15°C can be put in context by considering the ghost crab's biomechanics. At a T_b of 24°C, ghost crabs can only sustain an intermediate walking gait yet are able to trot and gallop at speeds comparable to that of a mammal of the same mass (Blickhan and Full 1987; Full and Weinstein 1992). A nearly three-fourths decrease in the MAS at 15°C makes only the very slowest walking gait sustainable. In the field, locomotor behavior of ghost crabs outside their burrows ceases when the temperature falls below 12°–15°C (Hughes 1966), which is presumably related to decreased locomotor capacity at these low temperatures.

The present study adds important dimensions to the general model used to predict the limitation of temperature on terrestrial locomotor performance in ectotherms. First, the data reveal that a decrement in $\dot{V}_{O_2 \max}$ at high temperatures can occur during quantified, steady state locomotion. Thermal optima of peak \dot{V}_{O_2} during uncontrolled activity are less likely to be caused by a submaximal effort at high temperatures rather than by a true thermal effect on \dot{V}_{O_2} . Second, C_{\min} can be temperature-dependent, but this effect in ghost crabs could not be separated from an elevated y-intercept of the $\dot{V}_{O_{2ss}}$ versus speed function. The decrease in $\dot{V}_{O_2 \max}$ at high temperatures did produce a very low MAS and endurance. However, MAS was higher than expected because C_{\min} was substantially reduced.

Given that T_b sets critical performance limits on sustainable locomotion, we wondered whether dehydration would do the same. In the present study, we forced the ghost crab to increase its T_b by restricting its ability to cool by evaporation. High T_b seriously impaired the ghost crab's ability to sustain locomotion. In less humid conditions, the ghost crab depressed its T_b by evaporative water loss. This reduction in T_b from 30°C to 24°C could be advantageous if water loss has less of an effect on locomotor performance than it does at high T_b . In a second study, we determine at what level or rate of dehydration sustained locomotor performance is compromised (Weinstein et al. 1994).

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