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The effects of temperature, desiccation, and body mass on the locomotion of the terrestrial isopod, *Porcellio laevis*

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ABSTRACT

Locomotion in terrestrial isopods is strongly influenced by body size and by abiotic factors. We determined the speeds of isopods of differing masses within a linear racetrack at temperatures ranging from 15 to 35 °C. We also predicted maximum speeds based on the Froude number concept as originally applied to vertebrates. In addition we used a circular thermal gradient to examine the temperature preferences of isopods, and we measured the effects of desiccation on locomotion. Measured speeds of the isopods progressively increased with temperature with an overall Q_{10} of 1.64 and scaling exponents ranging from 0.38 to 0.63. The predicted maximum speeds were remarkably close to the measured speeds at the highest test temperature although the scaling exponents were closer to 0.15. The isopods did not exhibit a strong thermal preference within the gradient; however, they did generally avoid temperatures above 25 °C. Moderate desiccation had no apparent effect on locomotor performance, but there was a progressive decrease in speed once animals had lost more than 10% of their initial body mass. Though largely restricted to moist habitats, *P. laevis* can easily withstand short exposures to desiccating conditions, and they are capable of effective locomotion over a wide range of temperatures. Since they are nonconglobating, active escape appears to be their primary defense when threatened under exposed conditions. Although their maximum speeds may be limited both by temperature and by their inability to change gait, these speeds are clearly adequate for survival.

1. Introduction

Locomotion is an essential behavior for almost all animals. It is needed for foraging, finding a mate, escaping predators, and, especially for ectotherms, for selecting a microhabitat with suitable temperature and moisture characteristics. The locomotor activity of most animals is, in turn, strongly affected by a variety of both abiotic and biotic factors such as ambient temperature, light, humidity, age, size, nutritional status, and health (Ossenkopp et al., 1996).

The terrestrial isopod, *Porcellio laevis*, is a cosmopolitan nonconglobating species (Powers and Bliss, 1983), which is restricted to relatively moist microhabitats. Soil moisture, in fact, appears to be the primary factor affecting both the distribution and the abundance of land isopods (Warburg et al., 1984). These animals respire by means of pseudotracheae or tree-lungs (Unwin, 1931), but they also rely heavily on integumentary respiration (Edney and Spencer, 1955). They lose water quite rapidly when not in contact with a moist substrate and, as in other land isopods, the rate of water loss increases with increasing temperature and with decreasing humidity of the surrounding air (Edney, 1951; Warburg, 1965).

Although the activity of terrestrial isopods is influenced by temperature, not all species respond in the same way (Warburg, 1993). *Porcellio* is among those genera that tend to aggregate at the lowest available temperature (Barlow and Kuenen, 1957). The activity of terrestrial isopods is also affected by the humidity of the air (Gunn, 1937), as is their locomotor speed (Waloff, 1941). However, there have apparently been no systematic studies of the effects of temperature, desiccation, and body mass on the locomotion of these crustaceans.

We designed the present study to examine the combined effects of ambient temperature and body size on the locomotor performance of *P. laevis*. To better interpret these results, we also investigated the temperature preferences of this species. We hypothesized that locomotor speed would progressively increase with both increasing temperature and increasing body mass. We further hypothesized that a methodology, developed for turtles and based on the Froude Number concept, of predicting the maximum speeds of animals unable or unwilling to change locomotor gait (Zani and Claussen, 1994), would be applicable to these terrestrial isopods. Finally, we hypothesized that isopod locomotion would be little affected by small changes in water content, but that below some critical level of water loss, speed would progressively decline until it approached zero at or near the point of ecological death. To more fully evaluate these results, we measured both ecological death, as defined by loss of the righting response, and the water content of normally hydrated individuals.

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2. Materials and methods

The isopods were maintained at room temperature (approx. 25 °C) in two bins containing rocks and other cover objects, moist soil, and a variety of vegetable scraps as a food source. For those studies where temperature was an experimental variable, a bin was moved to the constant temperature chamber one hour before the start of data collection to allow the animals to fully equilibrate to the testing temperature.

A 47 cm long, 1.5 cm wide and 1.5 cm tall aluminum racetrack was placed in the constant temperature chamber and used to measure locomotor performance. A strip of masking tape on the bottom of the track provided improved traction for the animals. Four infrared beams at 5 cm intervals crossed the track just above the level of the tape. These beams were attached to a custom designed electronic timer controlled by a Macintosh computer. The timer for the first 5 cm segment started automatically when a running animal intersected the first beam. Intersection of the second beam stopped the timer for the first 5 cm segment and started the timer for the second 5 cm segment, and so on. The shortest time for any 5 cm segment was recorded. The animal was placed on the track about 5 cm in front of the first beam and, if necessary, stimulated with a light touch to initiate a run. It was then retested two additional times following a brief (about 10 second interval). The shortest time was recorded for each run. The animal was then weighed to the nearest 0.1 mg on an electronic balance. The length and carapace height of the isopod were then measured with a caliper.

The speed of each individual isopod was calculated by dividing the distance traveled (5 cm) by the shortest amount of time for the three trials. Speeds were determined for approximately 50 individual isopods at temperatures of 15, 20, 25, 30, and 35 °C (±0.2 °C). The maximum speeds of isopods were predicted from the equation $V = (0.6\ g\ x\ h)^{0.5}$, where V = velocity in m/s, g = acceleration due to gravity, and h = hip height (Zani and Claussen, 1994). Since it was not practical to directly measure “hip height”, or in this case the effective leg length, for each individual isopod, we estimated this value from measures of carapace height. We defined effective leg length as the linear distance from the most proximal hinge joint to the ground, and we determined the relationship between this variable and carapace height by photographing running isopods through a glass (microscope slide) window in a special racetrack similar to that used for the speed measurements. Several lateral view photographs were taken for each of three isopods of different sizes (15.6, 38.1, and 73.6 mg). The photographs were then enlarged on a Macintosh computer and the appropriate measurements were taken.

The racetrack was also used to monitor the locomotor performances of isopods experiencing varying degrees of desiccation. The track was again placed in the constant temperature chamber, but only one temperature (25 ± 0.2 °C) was used. Prior to testing, animals were weighed and then placed overnight in small containers with a roll of dental cotton to which varying amounts of water had been added. The animals were reweighed on the day of testing and their speed was determined, as before, for three runs. Locomotor performance was evaluated in terms of body mass as a percentage of initial (fully hydrated) body mass.

Additional animals were dehydrated and weighed hourly until they were unable to right themselves within 30 s after being turned over on their backs. Their water content at this point of ecological death was recorded. Some animals were desiccated further until they first showed no sign of movement and their water content at this point of physiological death was also recorded. Finally, a subset of dead animals was dried at room temperature for over two weeks (when there was no further change in mass) to determine dry mass, from which we calculated initial water content.

To determine the temperature preferences of the isopods, we used a circular testing chamber, which consisted of a 20.0 cm (inside top diameter) inverted metal pie pan positioned in the middle of a 22.2 cm (inside bottom diameter) pan. This arrangement produced a 1.1 cm wide walkway around the pan. A clear plastic lid was marked off into 12 equal segments labeled A through L. Thermocouple thermometer probes were permanently positioned on the bottom of the walkway at the intersections of adjacent segments (e.g. A–B, B–C, etc.) and covered with a thin layer of folded and moistened Kimwipes. The chamber was then positioned with one end (centered at intersection A–B) on a rheostat controlled Cole Parmer Vela hot plate and the opposite end (centered at intersection G–H) on a Thermoelectic Stir Kool Model SK12 cold plate. The rheostat setting and the water flow through the cold plate were adjusted to create a gradient, when operating, of approximately 10 to 30 °C. For the control runs (no gradient established), an isopod was placed randomly at a given starting position. All lights, except for two overhead 25 W red bulbs, were then turned off and the investigator left the room. After exactly 30 min, the investigator returned to the room and, without turning on the lights, noted the position of the isopod within the walkway. The average temperature within the gradient chamber was then recorded and the isopod was removed and returned to its bin.

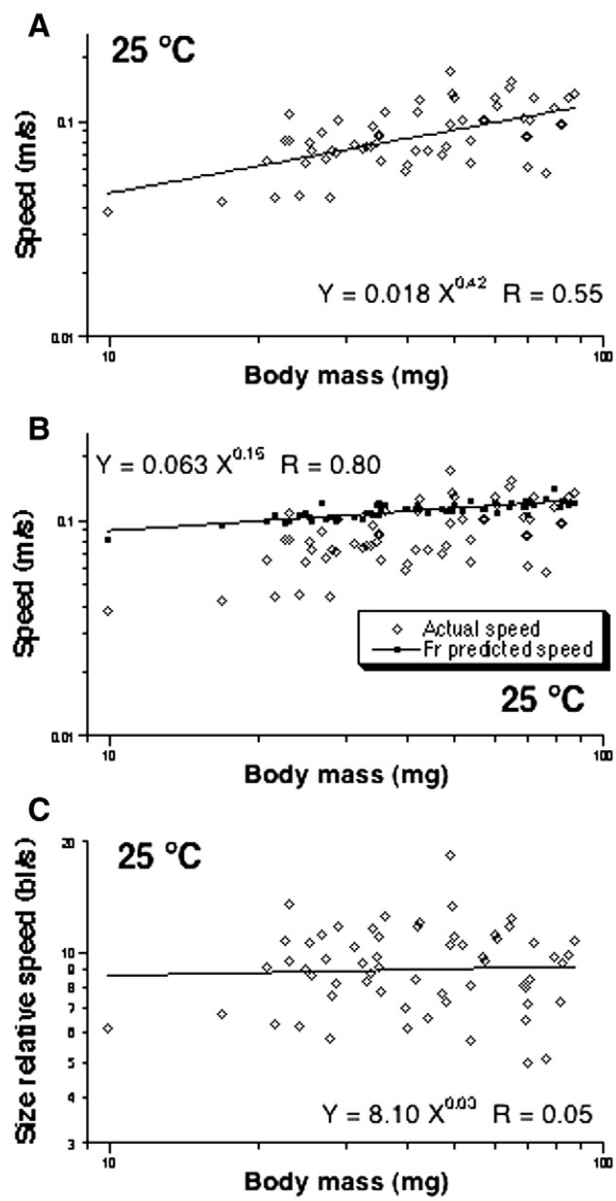

Fig. 1. The effects of body mass on the speeds of the terrestrial isopod, *Porcellio laevis*, at a temperature of 25 °C. Actual absolute speeds (A) are compared with maximum speeds predicted from estimated effective leg length and a Froude number of 0.6 (B). Size relative speeds, expressed as body lengths moved per second, are shown in C.