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Effect of thermal acclimation on preferred temperature, avoidance temperature and lethal thermal maximum of *Macrobiotus harmsworthi* Murray (Tardigrada, Macrobiotidae)

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Abstract

In order to understand thermal adaptation of the tardigrade *Macrobiotus harmsworthi*, and to test the optimality models, we measured preferred temperatures, avoidance temperatures and lethal thermal maxima of this species in an artificial thermal gradient after it was acclimated to either 2 °C or 12–22 °C for 2 weeks. The preferred temperature of the animals acclimated to 2 °C was 14 °C; the preferred temperature of the animals acclimated to 12–22 °C was 18.6 °C. There was significant difference between the preferred thermal intervals of animals acclimated to different temperatures ($F = 12.13$, $P = 0.00085$, df = 1, $N = 74$). There were two higher peaks in the preferred thermal interval of individuals acclimated to 12–22 °C. The avoidance temperature of the animals acclimated to 2 °C was 36 °C; the avoidance temperature of the animals acclimated to 12–22 °C was 35.1 °C. There was significant difference between the avoidance temperatures of the animals acclimated to different temperatures ($F = 23.562$, $P < 0.0001$, df = 1, $N = 34$). The minimum avoidance temperatures of the animals acclimated to either 2 °C or 12–22 °C were 0 °C. The lethal thermal maximum of the animals acclimated to 2 °C was 38.7 °C; the lethal thermal maximum of the animals acclimated to 12–22 was 38 °C. There was significant difference between the lethal thermal maxima of the animals acclimated to different temperatures ($F = 16.921$, $P = 0.000244$, df = 1, $N = 35$). Therefore, thermal acclimation imposed significant influence on the preferred temperatures, avoidance temperatures and lethal temperatures of *M. harmsworthi*. *M. harmsworthi* is an eurythermal species. The main results from our study support the optimality models.

Keywords: Thermal acclimation; Preferred temperature; Avoidance temperature; Lethal thermal maximum; Tardigrade; *Macrobiotus harmsworthi*

1. Introduction

All animals, from protozoans to mammals, avoid extremely high and low temperatures, showing a preference for intermediate range. When a thermal gradient is available, motile animals congregate within a narrow preferred thermal range. This phenomenon was termed behavioral thermoregulation or temperature preference (Reynolds and Casterlin, 1979). Fry (1947) gave a definition to the final preferendum as "a temperature around which all individuals (of a given species) will ultimately congregate, regardless of their thermal experience before being placed in a gradient".

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Thermal preference can reflect the optimal temperature required for some biological processes such as metabolism, movement, reproduction and growth (Dawson, 1975; Jobling, 1981; McCauley and Casselman, 1981; Kellog and Gift, 1983; Angilletta et al., 2002). Actually, animals often concentrate fitness-enhancing activities, such as growth, mating, reproduction and foraging, over a narrow thermal range (Andrewartha and Birch, 1954; Magnuson et al., 1979). It is therefore assumed that these fitness-enhancing activities are most efficient at the preferred temperature.

Since the pioneering study of Mendelssohn (1895), a variety of thermal gradients have been used to study the thermal preferences of various animals. However, very few studies have been published on the thermal preference of tardigrades. Papers describing the thermal adaptation of tardigrades mainly focus on cold tolerance (Westh and Hvidt, 1990; Raml and Westh, 1992, 2001; Sùmme and Meier, 1995; Sømme, 1996). A knowledge of the thermal requirements of aquatic organisms is very important since temperature is one of the main environmental factors that have a direct influence on physiology. To obtain an estimate of the optimum temperature for culture, we evaluated the preferred temperature, avoidance temperature and critical thermal minima and maxima of the tardigrade *Macrobiotus harmsworthi* Murray (Tardigrada, Macrobiotidae) acclimated to two different temperatures. The knowledge of the critical thermal minima (CTMin) and maxima (CTMax) provides a relevant ecological index since tardigrades in nature can meet such temperatures seasonally. Tardigrades distributed in temperate zones probably experience relatively low temperature in winter and high temperature in summer.

Traditionally, acclimation has been defined as the adjustment of physiological traits in response to changes in a single environmental variable in the laboratory (Prosser, 1991). Similarly, IUPS Thermal Commission (2003) gave the definition of acclimation as some physiological or behavioral changes occur within an organism, which reduces the strain or enhances endurance of the strain caused by experimentally induced stressful changes in particular climatic factors. Physiologists often assumed that all acclimation changes to the phenotype enhanced the physiological performance or fitness of an individual organism in the environment in which those changes were induced (Wilson and Franklin, 2002). The effect of thermal acclimation on the thermal preference, avoidance temperature and lethal thermal maximum has not previously been studied in a tardigrade.

Any environmental factor, such as a diurnal pattern of temperature, that follows an approximately sinusoidal trajectory through time will exhibit a bi- or trimodal distribution (Curry and Feldman, 1987). The optimality models modeled the bimodal environment as a mixture of two normal distributions sharing a common standard deviation and separated by an intermodal distance, and these models predicted that three fitness peaks would appear when the intermodal distance of the bimodally distributed temperature was 17 °C (Gilchrist, 1995). These models have not previously been tested in tardigrade.

Tardigrades, hydrophilous micrometazoans commonly called "water bears", are generally considered to be an independent phylum. Evidence from recent molecular studies with 18S RNA has shown that tardigrades are a sister group of the arthropods (Garey et al., 1996,1999; Giribet et al., 1996). Tardigrades show bilateral symmetry with four pairs of limbs that usually terminate in claws. Mature adults average 250–500 μm (Nelson and McInnes, 2002). Tardigrades have a complete digestive system, a complete reproductive system and a fluid-filled body cavity (hemocoel) that functions in circulation and respiration. The nervous system consists of a dorsal lobed brain and ventral nerve cord with fused paired ganglia. Molting occurs periodically throughout the life of a tardigrade (Walz, 1982). Freshwater eutardigrades are usually gonochoristic but usually with parthenogenesis. All active individuals require a film of water around the body. They could be found in permanent freshwater habitats, in sea, river or lake sediment, in littoral zone or in moist mosses. Most tardigrade species are terrestrial, occurring in moist soil and leaf litter, or among mosses, lichens, liverworts, and cushion-shaped flowering plants (Ramazzotti and Maucci, 1983; Kinchin, 1994). Tardigrades can endure extremely low temperatures; some species have even survived absolute zero (Westh and Hvidt, 1990; Raml and Westh, 1992, 2001). The fact that tardigrades have a strong ability to resist very low temperature, however, does not mean that they can live at any temperature. Actually a change in environmental conditions can induce the animal to enter a cryptobiosis (Crowe, 1975; Nelson and McInnes, 2002), which can be anhydrobiosis, anoxybiosis, cryobiosis or osmobiosis (Crowe, 1975). Cryobiosis enables tardigrades to survive freezing and thawing, and is the principal survival strategy of limno-terrestrial tardigrades living in very cold environments (Sømme, 1996). The formation of tuns also plays a role in the dispersal of cryobiotes.

This study aimed to obtain an estimate of the optimum temperatures, to estimate the effect of thermal acclimation on the preferred temperatures, avoidance temperatures and lethal thermal maxima of the tardigrade *M. harmsworthi*, and to test the optimality models.

2. Materials and methods

Tardigrades, *M. harmsworthi* Murray were collected from samples of mosses growing on rocks and soil from