Locomotor activity in *Branchipus schaefferi* (Fischer, 1834) (Branchiopoda: Anostraca) under thermal variation

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ABSTRACT

The behavioral responses of *Branchipus schaefferi* Fisher, 1834 males and females to short-term thermal stress in six different rearing conditions are studied. The swimming performance was tested in pure tap water and water collected from both male and female culture mediums. The animal's behavior was recorded using a high-definition digital video camera mounted approximately 30 cm above the experimental containers. The swimming track and the thoracopod beating rates were recorded manually for each animal at different temperatures. The results indicate that in most cases, a significant increase in active swimming and limb beating rate occurred with increasing temperature. However, the animals tested in the different male and female culture medium were significantly less active compared to those in tap water, under similar thermal stress. Animals seem to produce substances in the culture media that influence their locomotor behavior under thermal stress.

KEYWORDS

Anostraca, beating rate, behavior, locomotion, thermal stress

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INTRODUCTION

Temperature is a key abiotic variable that can influence the behavior of various taxa in both terrestrial and aquatic habitats (Barnes *et al.*, 2001) and fluctuates seasonally, on a daily or even an hourly basis (Lagerspetz and Vainio, 2006). Organisms capable of locomotion avoid extreme temperatures, even though what is "extreme" varies depending on the species, its evolutionary thermal history and the thermal history of the individuals studied. The effects of genetic transmission and individual physiological experiences will influence the thermal behavior of an organism (Lagerspetz and Vainio, 2006). Poikilotherms are particularly sensitive to temperature because each temperature increase leads to a multiple expansion in metabolism (Barnes *et al.*, 2001).

Temporary waters have much greater physical and chemical amplitudes than most permanent ponds and streams. They are usually shallow and characteristically unstable with respect to abiotic conditions, since they can be strongly heated by the sun and cooled at night (and also by wind). Thermal variations may be as much as 25 °C within 24 h (Williams, 2006: 30, 31). Therefore, the organisms that live in these types of habitat have to be very adapted to these conditions if they are to persist.

Crustaceans are a diverse and ancient group of arthropods that have long been studied as interesting model systems in biology, especially for understanding animal evolution and physiology and for environmentally relevant studies (Thiéry, 1991). The swimming behaviour of crustaceans may be affected by many factors, like water temperature, population density, or the presence of predators (Lindstrom and Fortelius, 2001; De Robertis *et al.*, 2003).

In crustacean ecology, models are from a wide range of swimming behaviors related to the species, age, prey density, presence of a predator or conspecific individual, the sex of individuals and the information provided in the surrounding water by swimming animals (Seuront *et al.*, 2004). Branchiopoda colonize these habitats successfully and they are adapted to live in waters exposed to very rapid and sudden physical and chemical changes (Beladjal *et al.*, 2007).

They move through the water in ways that differ strongly between orders, families and genera (Dumont and Negrea, 2002). Anostracans swim slowly and ventral side-up through open water but sometimes they may descend to the bottom and scrape through the sediment. When disturbed, they are capable of short darts and abrupt changes of direction, which probably correspond to predator escape tactics. Swimming depends on the continuous, metachronic beat of foliaceous appendages. The beating rate varies with age and with environmental influences, most notably temperature (Thiéry, 1997).

Branchipus schaefferi Fisher, 1834 lives in shallow ephemeral pools in the Mediterranean area, the Sahara Desert, and central Europe (Petkovski, 1997; Cvetković-Miličić, *et al.*, 2005; Beladjal and Mertens, 2017; Mioduchowska *et al.*, 2018). It produces resting eggs that undergo diapause in dried pools and is capable of withstanding a high-temperature environment. The temperature that resting eggs have to endure can be as high as 80 °C (McFadden *et al.*, 2005), and they may survive up to 110 °C under experimental conditions (Beladjal *et al.*, 2008; Mertens *et al.*, 2008). They survive the dehydration stress and the high temperatures and when the pools are filled with water again, they hatch and initiate a new generation of fairy shrimps (Fryer, 1996; Jönsson and Järemo, 2003; Gyllström and Hansson, 2004; Beladjal *et al.*, 2007; Atashbar *et al.*, 2012; 2014).

Temperature variation is the main factor influencing the thermal behavior responses, but there might also be some other factors such as presence of individuals of the opposite sex or adult waste products containing semi-chemical substances acting as the supplementary determinants. These animal metabolites may be used as pheromones in urine or other excretory pathways to regulate thermal behaviors. Pheromones are often divided according to their function into sex, aggregation and alarm pheromones (Wyatt, 2003). When water from *Branchinecta lindahli* Packard, 1883 female cultures was added to fully isolated males, they began immediately to exhibit behavior that indicated they were looking for females, thus proving the presence of pheromones (Rogers, 2019).

Therefore, it seems that the anostracan breeding environment can affect the quantity and quality of behavior of these animals against thermal changes. Based on this supposition, the present study was carried out to characterize the behavioral response of *B. schaefferi* to short term thermal stress under six different rearing conditions composed of tap water and water collected from both male and female culture mediums.

MATERIAL AND METHODS

Mud containing cysts of *B. schaefferi* was collected in the hot arid area of the Jbilet Mountains, 25 km north of Marrakech (31°6'30''N 8°24'00''W), Morocco. The sample containing ~300 eggs was dipped in distilled water (pH = 6.55, EC = 0.05 µS/cm) in a 1-L beaker and incubated for 24 h under controlled conditions in the laboratory (23 °C ± 1 °C, day/night light cycle: 14:10). Newly hatched nauplii were collected, reared in aerated tap water (pH = 7.5, Electrical conductivity (EC) = 320 µS/cm) and fed unicellular algae (*Scenedesmus* sp.). Male and female adults were separated one week before the thermal experiments. The thermal behaviors were measured under the following treatments: 1) males in tap water (MT), 2) females in tap water (FT), 3) males in the presence of females in tap water (MFT), 4) females in the presence of males in tap water (FMT), 5) males in the medium that females were raised in (MFM) and 6) females in the medium that males were raised in (FMM). To provide the male-only and female-only medium a portion of each of their own culture media was separately filtered using a 100 µm mesh net. The fairy shrimps were transferred into plastic containers (10 × 20 × 5cm), filled to a depth of one centimetre with fresh tap water or the rearing medium. The containers were placed in a water reservoir at a constant temperature of 23 °C (± 1 °C). During the experiment, the increasing and decreasing of temperature was achieved slowly (0.1°C/min to a minimum of 2 °C and a maximum of 41 °C) and was maintained for 3 to 3.5 h. Ten adult males and females were used for testing the thermal resistance, beating rate and motor activities in each experimental group. Median lethal temperature (LT_{50}), critical thermal maximum (CTmax) and critical thermal minimum (CTmin) were recorded. The behavioral responses were recorded using a high-resolution digital video camera (Sony HDR-CX240) mounted approximately 30 cm above the containers. The recorded videos were viewed at low speed to determine the direction of motion and the limb beating rate. Distances covered by the specimens were drawn on a laptop screen manually and the beating rate was counted visually for 10 seconds. Six to seven measurements were averaged for each animal at different temperatures. Drawings were later digitized using a Summa Sketch III professional digitizing table. The results were statistically analysed using SPSS (version 13) analysis of variance (one-way ANOVA) and $p < 0.05$ was chosen as the significance level.

RESULTS

Both sexes become more active at higher temperatures by increasing swimming activities and limb beating rate, while the opposite was observed at low temperatures in all test environments (Tabs. 1, 2). The highest limb beating rate was recorded at 40 °C and was 8.89 ± 0.19 beats per seconds for females in tap water (FT) and 9.07 ± 0.18 beats/s for males in the presence of females (MFT) (n = 30). The lowest beating rate was recorded at 2 °C for males in the female medium (MFM) (0.12 ± 0.05 beats/s), and for females in the male medium (FMM) (0.26 ± 0.06 beats/s). Significant differences in limb beating rate were found between males and females and also between each sex at most temperature treatments. In most cases, the beating rate was higher in males than females (p <0.05) (Tab. 1).

The general pattern of the limb beating speeds for the different temperatures is shown in Fig. 1. In all groups, the limb beating rate started to decline below 25 °C.

Maximum swimming activities were recorded at 30 °C for males in the presences of females in tap water (MFT) (4.79 ± 0.29 cm per seconds) and for females in the presences of males also in tap water (FMT) (3.06 ± 0.16 cm/s), whereas minimum activity was noted at 5 °C (0.02 ± 0.00 and 0.001 ± 0.004 cm/s) for males and females in each culture media

(MFM and FMM) respectively (Tab. 2). The fairy shrimps remain stationary at 2 °C with limbs beating at a slow rhythm, but no forward movement was recorded (Tab. 2). A similar behavior occurred for both sexes, since the shrimps laid almost motionless besides the container walls. They tend to aggregate before becoming completely immobile at the lowest temperature (2 °C), whereas they prefer to be away from each other at higher temperatures (35 and 40 °C). The minimum displacement value of movement was recorded for females in the male culture water (FMM) (Fig. 2, Tab. 2). Significant differences were observed in the movement of both sexes in the culture media compared to the other temperature conditions (Tab. 2). Maximum and minimum distances covered by females in the male culture medium were observed at 25 °C (2.26 ± 0.05 cm/s) and 5 °C (0.001 ± 0.004 cm/) respectively. Similarly, the maximum and minimum distances covered by males in the female culture medium were observed at 20 °C (1.23 ± 0.09 cm/s) and 5 °C (0.02 ± 0.00 cm/s) respectively (Tab. 2).

A significant difference between the groups was found in their CTmax. The incipient upper lethal temperature in the experiment using the culture media was observed at 40 °C compared to 38–39 °C in other groups. The maximum temperature tolerated by the animals was slightly higher than the incipient upper lethal temperature, but none of the shrimps survived at 41 °C in all groups. The median lethal temperature (LT_{50}) was between 39 and 40 °C. The mortality rate quickly increased with increasing water temperature to 41 °C, which is a lethal condition for both sexes. Almost all specimens (90 %) that were completely immobile at CTmin (1–2 °C), recovered after the temperature was increased to the initial one (23 °C).

Table 1. Limb beating rate (beats/sec) (mean ± Standard Deviation) of *Branchipus schaefferi* under different temperatures. (MT: males in tap water; FT: females in tap water; MFT males in the presence of females in tap water, FMT: females in the presence of males in tap water; MFM: males in female medium; FMM: females in male medium).

Temp (°C)	MT	FT	MFT	FMT	MFM	FMM
2	1.16 ± 0.05[b]	1.93 ± 0.08[d]	1.55 ± 0.05[c]	1.21 ± 0.04[b]	0.12 ± 0.05[a]	0.26 ± 0.06[a]
5	2.13 ± 0.07[c]	2.21 ± 0.06[c]	2.14 ± 0.05[c]	1.85 ± 0.03[b]	1.21 ± 0.05[a]	1.88 ± 0.06[b]
10	2.47 ± 0.05[b]	2.82 ± 0.07[c]	2.53 ± 0.06[b]	2.39 ± 0.05[b]	2.09 ± 0.05[a]	2.44 ± 0.06[b]
15	3.53 ± 0. 13[bc]	3.08 ± 0.07[ab]	4.96 ± 0.09[d]	4.66 ± 0.13[d]	2.75 ± 0.07[a]	3.66 ± 0.16[c]
20	4.46 ± 0.09[b]	4.39 ± 0.12[b]	6.54 ± 0.14[c]	6.35 ± 0.31[c]	3.01 ± 0.08[a]	4.69 ± 0.15[b]
25	7.57 ± 0.18[b]	7.44 ± 0.28[b]	7.34 ± 0.12[b]	6.70 ± 0.26[b]	5.38 ± 0.24[a]	4.98 ± 0.24[a]
30	7.79 ± 0.18[bc]	8.76 ± 0.68[c]	7.98 ± 0.15[bc]	7.30 ± 0.26[b]	5.44 ± 0.24[a]	4.62 ± 0.19[a]
35	8.45 ± 0.32[c]	8.83 ± 0.29[c]	8.07 ± 0.14[bc]	7.08 ± 0.26[b]	5.09 ± 0.21[a]	5.45 ± 0.19[a]
40	8.08 ± 0.15[c]	8.89 ± 0.19[cd]	9.07 ± 0.18[d]	6.97 ± 0.21[b]	6.41 ± 0.24[ab]	6.01 ± 0.22[a]

Values with the same superscripts in the same row are not significantly different at the 5 % level

Table 2. Swimming activity (cm/sec) (mean ± Standard Deviation) of *Branchipus schaefferi* under different temperatures. (MT: males in tap water; FT: females in tap water; MFT males in the presence of females in tap water, FMT: females in the presence of males in tap water; MFM: males in female medium; FMM: females in male medium).

Temp. (°C)	MT	FT	MFT	FMT	MFM	FMM
2	0.00 ± 0.00[a]	0.00 ± 0.00[a]	0.00 ± 0.00[a]	0.00 ± 0.00[a]	0.00 ± 0.00[a]	0.00 ± 0.00[a]
5	0.35 ± 0.05[c]	0.09 ± 0.04[b]	0.24 ± 0.05[bc]	0.21 ± 0.05[abc]	0.02 ± 0.00[a]	0.001 ± 0.004[a]
10	1.47 ± 0.08[b]	0.45 ± 0.06[a]	1.03 ± 0.11	1.59 ± 0.09[b]	0.45 ± 0.05[a]	0.36 ± 0.05[a]
15	1.71 ± 0.11[c]	1.22 ± 0.08[b]	2.31 ± 0.08[cd]	2.03 ± 0.12[d]	0.69 ± 0.11[a]	1.15 ± 0.06[b]
20	2.33 ± 0.16[cd]	2.13 ± 0.14[bc]	2.74 ± 0.24[cd]	2.22 ± 0.14[d]	1.23 ± 0.09[a]	1.60 ± 0.06[ab]
25	2.51 ± 0.11[c]	2.66 ± 0.11[c]	3.68 ± 0.21[d]	2.61 ± 0.13[c]	0.72 ± 0.12[a]	2.26 ± 0.05[b]
30	2.64 ± 0.14[c]	2.06 ± 0.12[c]	4.79 ± 0.29[e]	3.06 ± 0.16[d]	0.67 ± 0.10[a]	1.61 ± 0.05[b]
35	3.39 ± 0.17[d]	1.46 ± 0.11[ab]	4.12 ± 0.26[e]	2.45 ± 0.11[c]	0.98 ± 0.1.9[a]	1.90 ± 0.09[bc]
40	2.86 ± 0.21[cd]	2.12 ± 0.13[b]	3.55 ± 0.27[bc]	2.24 ± 0.18[d]	0.92 ± 0.17[a]	0.72 ± 0.07[a]

Values with the same superscripts in the same row are not significantly different at the 5 % level
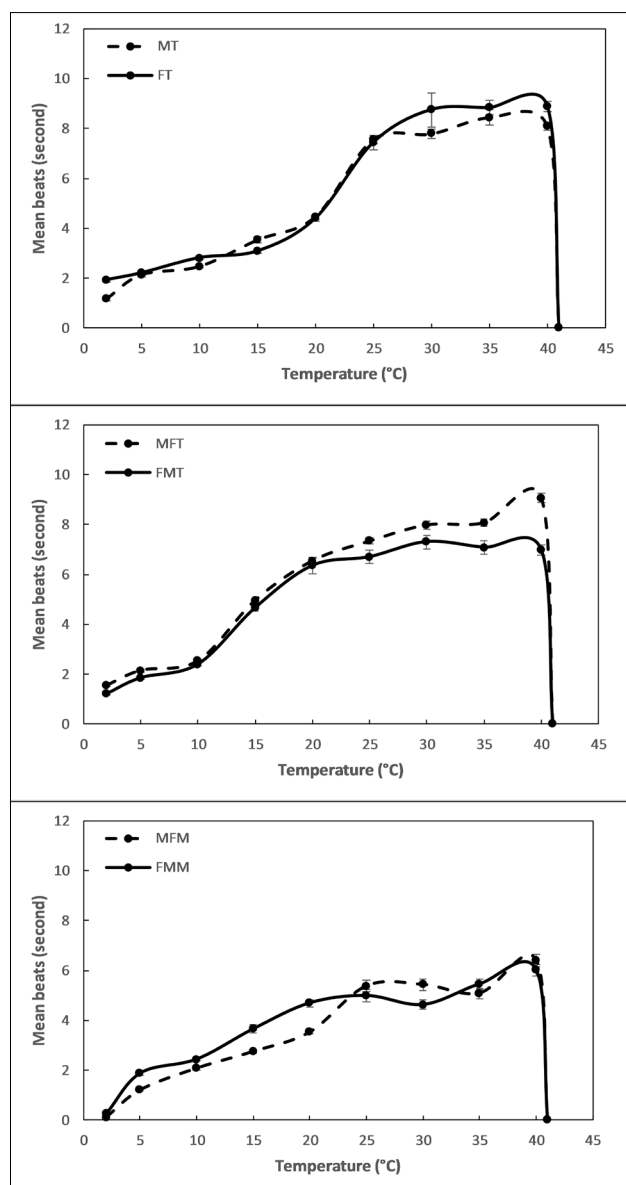
Figure 1. Compression of limb beating rate of male and female *Branchipus schaefferi* under different culture treatments. (MT: males in tap water; FT: females in tap water; MFT males in the presence of females in tap water, FMT: females in the presence of males in tap water; MFM: males in female culture medium; FMM: females in male culture medium).

Figure 2. Comparison of swimming activities between male and female *Branchipus schaefferi* as a function of different temperatures and culture conditions (MT: males in tap water; FT: females in tap water; MFT males in the presence of females in tap water, FMT: females in the presence of males in tap water; MFM: males in female culture medium; FMM: females in male culture medium).

DISCUSSION

The abiotic and biotic environmental conditions, according to the present work, are determinative for *B. schaefferi* behavior. Thermal resistance patterns indicate that this species belongs to the eurythermic warm water group that has a wide range of temperature tolerance. Perhaps, the ability of *B. schae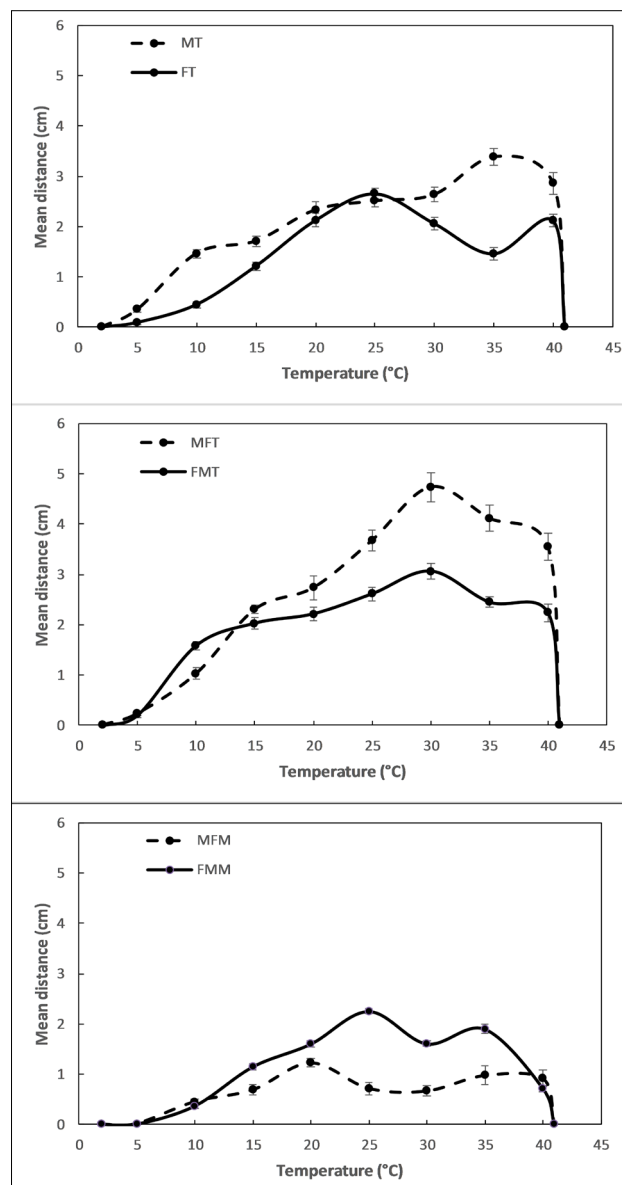fferi* to tolerate higher and lower temperatures is typical, and then it may explain the wide distribution of this species.

We found that the animals tolerate wide variations in temperature (ranges 1 to 39 °C), and survival is possible only during short-term exposure to 40 °C which was registered as maximum temperature tolerance by *B. schaefferi*. The highest recorded natural water temperature is ~35 °C in relatively shallow habitats (Vanschoenwinkel *et al.*, 2013).

In general, a reduction in ambient temperature is immediately followed by a decrease in muscular performance in *Daphnia* O.F. Müller, 1785. For example, the limb beating rate decreases, which in turn reduces the uptake of oxygen and food (Schwerin *et al.,* 2009). High temperatures cause a direct metabolic effect on the shrimp resulting in greater speed of locomotion (Abdullah, 1961). Swimming activity varies with the temperature gradient, as well as limb beating rate, but they are not necessarily identical. This means that the increase in limb beating rate does not always match with increasing movement. For example, there is a considerable decrease in movement between the two peak temperatures (25 and 40 °C) in females but the limb beating rate remains the same or only slightly increases. Apparently, this is caused by hypoxia in the medium, as more oxygen is required to satisfy the animal needs with increasing metabolic rate, as a consequence of the temperature increase. In this case, fairy shrimps try to reduce energy consumption resulting in a decrease in oxygen demand.

This is a trade-off between the temperature and oxygen needs of the fairy shrimps as they attempt to reduce oxygen consumption by remaining motionless. The swimming and then remaining temporarily motionless behavior are repeated alternately. Ultimately, with increasing temperature towards the higher critical point, these shrimps try to avoid such intolerable conditions with increasing displacement activity (Fig. 2). Based on our results, in most cases, a significant increase in active swimming appeared with increasing temperature, which in view of the lesser activity at lower temperatures, can be inferred as an escape response to avoid over-heating.

Our results provide evidence that thermal-induced pheromones may be responsible for controlling anostracan limb beating rates which consequently affect swimming activity. The pheromones either induce aggregation, separation or escape behaviors in shrimp during critical thermal conditions. These behaviors were observed in all experiments, however, they were more prominent in the experiments using opposite sexes (MFT and FMT). The visibility and the pheromone concentration might play an important role in the intensification and modification of locomotor responses. There is a significant increase in swimming activities that might have been induced by visual stimuli (p <0.05), however, it seems that the swimming activities are harmonized by some other factors dissolved in the culture media (Fig. 1). The harmonization is much more prominent in males compared to females and is probably due to the presence of chemicals produced by the females. Comparison of the results obtained from the experiments using tap water and adult culture media water shows that male movement intensity changes are much larger than females at all temperatures.

Changes in environmental conditions affect the locomotor patterns of *B. schaefferi* in terms of type and velocity of movement. Locomotor performance can easily be explained by kinetic responses, such as changes in specific locomotor intensity in response to unstable environmental factors (Anufriievaa and Shadrin, 2014). On the other hand, the effect of temperature variations on behavior of the fairy shrimps is largely based on individual responses to pheromone-like substances produced by them. Males are, for instance, more active and highly influenced by the environmental conditions than females. Most studies of gender differences in gammarids (Crustacea, Amphipoda) have shown a higher sensitivity of females to stress (Kinne, 1953; McCahon and Pascoe, 1988; Sornom *et al.*, 2010). Similarly, and according to Buikema and Benfield (1979), the difference in sensitivity between both sexes of gammarids could partly be explained by an increase in metabolic energy demands during oogenesis and egg incubation, and the subsequent increase in lipid synthesis and mobilization, in comparison to spermatogenesis processes which are less demanding in terms of energy. In related studies in decapod crabs, one of the reasons that a change in external conditions such as temperature might change the "strength" of personality in hermit crabs is that individuals can vary the way they respond to the changing factors (Briffa *et al.*, 2008; 2013).

Brine shrimp seem to produce substances that influence their locomotor behavior under thermal variation. They aggregate at low temperature and disperse under increasing temperature. It seems that pheromone-like substances in the culture media increase the heat tolerance of fairy shrimps, improve their survival at low temperatures (1–2 °C) and their acclimation to the wide range of temperature variations. The chemical metabolic products of adult

females at increased temperature proved to be very important in decreasing male motor activities and energy consumption. In conclusion, the identification of the tolerance range of abiotic conditions, such as temperature, could be useful in modeling species distributions on a regional or global scale. Further work is needed to determine the precise role of visual and semio-chemical factors on fairy shrimp thermal behavior.

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