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Reduction of Optimal Thermal Range in Aging Western Cherry Fruit Flies (Diptera: Tephritidae)

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ABSTRACT. The western cherry fruit fly is an economically important pest of sweet cherries in the western United States. The potential of this pest to establish and spread in areas in which it is not currently present has been the focus of recent research. Most published information on the thermal tolerance and optimal thermal range of this pest has focused primarily on the diapausing pupae and predictive phenology models. Microrespirometry and differential calorimetry can be useful tools in describing the thermotolerance and optimal thermal range of insects. This methodology was employed to investigate the effects of western cherry fruit fly adult age on the optimal thermal range. Newly emerged flies exhibited the widest optimal thermal range spanning from 6.6 to 42.2°C for a total range of 35.8°C during heating scans of 0.4°C/min from 2 to 50°C. This range diminished as the flies aged, with the shortest span observed with 28-d-old flies ranging from 10.5 to 37.8°C, a span of 27.2°C. Measurements of heat rate and oxygen consumption at isothermal, or static, temperatures indicated that all flies could survive exposure to 40°C for at least 20 min, and that metabolism was greatly reduced, with a concomitant reduction in oxygen consumption rate at 40 to 42°C. All flies exhibited a heat rate and oxygen consumption rate of zero when exposed to 45 and 50°C. The loss of thermotolerance in adult flies can influence its ability to establish and spread in climates where daily temperatures exceed the optimal thermal range of this species.

Key Words: differential scanning calorimetry, microrespirometry, optimal thermal range, thermal tolerance

The western cherry fruit fly, *Rhagoletis indifferens* (Curran) (Diptera: Tephritidae) is an economically important pest of sweet cherries, *Prunus avium* (L.), in the western United States (Yee et al. 2014). There is a zero tolerance for the presence of this pest in commercially produced sweet cherries, and lots identified as containing a single larva can be rejected from the packing house and the grower is at risk of losing packing house services if another larva is identified in another lot (Brown 2009). In addition, shipments from lots found to contain a single larva may not be made to California, which enforces a strict quarantine against this pest (CDFA 2012).

The zero tolerance for the presence of western cherry fruit fly in commercially produced sweet cherries has necessitated the extensive application of monitoring and pest control activities that are costly to the grower, and in nonorganic production programs, risks exceeding MRLs (minimum residue levels) for pesticides on the fruits. Regardless of this practice of rejecting lots with single larval finds, other countries require additional postharvest quarantine procedures, including fumigation with methyl bromide, to provide extra protection against the accidental introduction of this pest.

Recent research using ecological niche modeling (Kumar et al. 2014a,b) indicates that the current and potential distribution of this pest is limited by abiotic factors, such as upper summer temperatures and duration of winter temperatures below 5°C. The development of these models and their predications relied on the published upper and lower thermal tolerances of this pest as well as the climate within the regions where this pest is known to occur. The current published thermal tolerances of this pest have been focused on the tolerance of the longest lived developmental stage, the diapausing pupae (AliNiazee 1975; van Kirk and AliNiazee 1981; Stark and AliNiazee 1982). However, there is no information on the effects of temperatures on the metabolism of adult flies, the stage most important in establishing new infestations and spreading the distribution of the species. In a review by Bowler and Terblanche (2008), they stated that "The implication for biogeography is that one or many life stages, perhaps the most temperature sensitive, may set the geographic distribution limit for a species". Thus, it is important to determine the thermal range of the adults, which may be the most thermally sensitive developmental stage of this species.

Differential scanning calorimetry and microrespirometry can provide useful information on the thermal tolerance of a pest and can be related back to the phenology of the species (Neven and Hansen 2010; Neven et al. 2014; Terblanche et al. 2011). Establishing the upper and lower limits to growth and development, referred to as Pejus temperatures (pejus, Latin, for 'turning worse') (Pörtner 2001), can be useful in determining the optimal range of environmental temperatures in which a species can survive. This range can then be used in ecological niche models to optimize the predictive capabilities of the models and more accurately identify those regions most at risk of an introduced species to establish and spread. This study was performed to facilitate the refinement of predictive ecological niche models that were developed using thermal tolerances of pupae to identify areas within the United States and throughout the world most at risk of western cherry fruit fly establishment through accidental introduction (Kumar et al. 2014a,b).

Materials and Methods

Insects. Sweet cherries infested with western cherry fruit fly larvae were collected from several sites along the Yakima and Columbia River valleys in 2012–13. Infested sweet cherries were collected from unmanaged, unsprayed back yard trees on a weekly interval from 15 June to 25 July in both years. The infested fruits were brought back to the USDA-ARS Yakima Agricultural Research Laboratory for pupal collection. Infested sweet cherries were suspended over ~100 g soil mixture (3:2:1 peat moss:sand:water) with an in-house constructed wire mesh (1.27 cm mesh) bottom tray (L × W × H 43.2 × 30.5 × 10.2 cm) suspended 1.27 cm above the soil with 1.27 cm OD PVC tubing in a standard restaurant bussing tub (TRAEX, Liberty Food Service Co., Daine, WI) (L × W × H 45.1 × 33 × 17.8 cm). Soil containing third instars and pupae were collected daily for 7 d. Pupae in soil were held at

23°C, 16:8 (L:D), 40% relative humidity (RH) for 15 d following the last collection. Pupae were separated from the soil, counted, and placed in groups of 100 pupae in 30 ml deli cups with 15 ml fresh soil mixture, and placed in a 3°C cold room for 6 mo. After the 6 mo cold exposure period, one cup with pupae was removed each week for a 8 wk period and held in a screen cage enclosure (L × W × H 30.5 × 30.5 × 30.5 cm, 929 cm^3) at 23°C, 16:8 (L:D), and 40% RH until they emerged. Freshly, eclosed flies were individually aspirated and moved into a new tent cage within the same environmental control room with artificial diet and a water source (Yee 2003a, Yee and Chapman 2009), until collected for analysis.

Flies used for calorimetry and microrespirometry tests were collected at 1, 7, 14, 21, and 28 d following eclosion. Flies were placed into groups of five flies of a single sex into a 20 ml glass vial with the top sealed with cork. The sealed vials with flies were weighed on a microbalance prior to chilling. Flies were chilled for 5 min at 5°C to reduce movement and facilitate placement into the calorimeter ampoules. The vials and corks were weighed again and the total weights of the flies were calculated prior to placement of the ampoules into the calorimeter.

Differential Scanning Calorimeters (DSCs). An MC-DSC Model 600000 multicell differential scanning calorimeter (TA Instruments, Inc. New Castle, DE) with two sets of 1.0 ml Hastelloy ampoules, 11 mm diameter by 5 mm deep, was used for the measurement of metabolic heat rate. One set of ampoules is fully sealed; the other set is modified to accommodate 3 mm OD PEEK tubing for insertion of an oxygen sensor (described later). The MC-DSC has a detection limit of 0.2 µW and baseline repeatability of 2 µW. The MC-DSC was operated with the MC-DSCRUN (v. 2.9.10, TA Instruments 1996, 2007) program.

Oxygen Sensors. FOXY-PI600-2 M oxygen sensors connected to Neo-Fox spectrophotometers (Ocean Optics, Dunedin, FL) were inserted into the three sample ampoules of the MC-DSC. The Neo-Fox units were operated with the Neo-Fox Viewer (v. 2.40, Ocean Optics, Inc. 2010). A two-point calibration of the sensors was performed each day with N_2 (0% O_2) and air (21% O_2). Oxygen readings were obtained for each isothermal temperature by injecting 1 ml of fresh room air, to provide a more accurate measurement of O_2 consumption, into the ampoule after the µW readings in each ampoule had reached a steady state, on average 10 min at the target temperature. The oxygen levels were recorded and a 5 min reading was used to calculate oxygen consumption rate.

Scans. Continuous temperature scanning measurements of metabolic heat rates were made from 5 to 50°C at a rate of 0.4°C/min. Five flies of a single sex were used in each ampoule for each scan. Each scan was replicated four times with three ampoules per replicate. Scans were performed on 1-, 7-, 14-, and 21-d-old flies because these ages are within the normal expected life span of flies in the field (Yee 2003b).

Isothermals. Constant temperature heat rates and oxygen consumption rates were measured at several temperatures from 2.5 to 42°C for durations of 20 min at each temperature. Heat rate data were collected for 2,400 s after a 600 s equilibration step at each temperature. The rate of temperature increase between isothermals was set to 1°C/min. Isothermal data were also collected in separate experiments at 42, 45, and 50°C for 2,400 s with a 600 s prior equilibration step. Each isothermal measurement was replicated four times with three ampoules per replicate. Simultaneous oxygen readings were obtained at each isothermal temperature, as previously described. Isothermal heat rates and oxygen consumption rates were performed on 1-, 7-, 21-, and 28-d-old flies because in preliminary experiments there were few differences between isothermal rates of 7- and 14-d-old flies and 28-d-old flies are on the upper extreme age for flies in the field (Yee 2003b). At the end of each experiment, the flies were removed from the ampoules and the ampoules cleaned and dried according to the manufacturer specifications.

Calculations. Metabolic heat rates during continuous temperature scanning were calculated following the equation from Hansen and Criddle (1990):

$$(dQ/dt)\text{metabolism} = (dQ/dt)\text{measured} - (dQ/dt)\text{baseline} + (\text{Csample})(dT/dt) \quad (1)$$

where (dQ/dt) is heat rate, (dT/dt) is the temperature scan rate, and Csample is the heat capacity of the sample. Csample was calculated with the equation:

$$\text{CSample} = \text{Specific heat capacity} * \text{mass of sample or } (4.218\,\text{J}\,^{\circ}\text{C}^{-1}\text{g}^{-1})\,(\text{mass of sample}) \quad (2)$$

where the specific heat capacity was determined with four replicate scans from 0 to 50°C of three ampoules each containing an average 60 mg of dead adult flies of each age. Heat capacity was calculated as:

$$\text{Specific heat capacity} = (dQ/dt)\text{measured} - (dQ/dt)\text{baseline})/[(dT/dt * \text{g sample})] \quad (3)$$

The oxycaloric ratio was calculated by dividing the metabolic heat rate at each isothermal temperature by the moles of oxygen consumed at each temperature. Values below Thorton's constant, 470 kJ/mole O_2, indicate normal aerobic metabolism, whereas ratios significantly higher than Thorton's constant indicate anaerobic metabolism (Hansen et al. 2004).

Statistics. All DSC data were initially analyzed using the NanoAnalyze program (V.2.2.0 Copyright 2005, 2011 TA Instruments) to obtain (dQ/dt) and (dT/dt) values. These data were then analyzed according to Equations (1), (2), and (3) with Excel (V.14.0.6112.5000, Microsoft Office Standard 2010). Averages, standard deviations of the mean, and standard error of the mean were calculated using Excel. ANOVAs, multiple and one-way ANOVAS, were performed using Sigmaplot (for Windows Version 12.3, 2011 Systat Software, Inc). Ranking of means was performed using either the Duncan's Method or the Holm-Sidak method of all pairwise multiple comparisons procedure (for Windows Version 12.3, 2011 Systat Software, Inc).

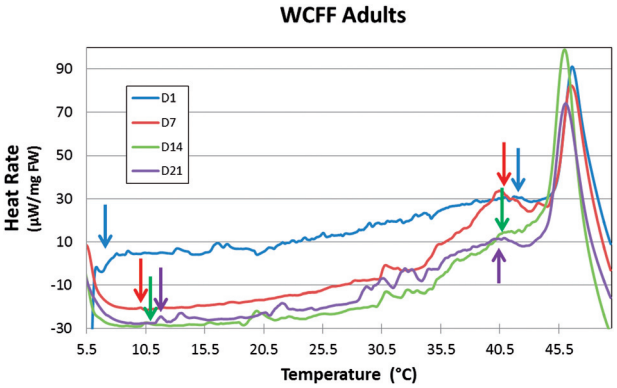

Fig. 1. Effects of continuous scans on the metabolic heat rate of 1- (Blue), 7- (Red), 14- (Green), and 21 (Purple)-d-old western cherry fruit flies. Depicted scans are from a single run for each age to reflect variation. Each scan was replicated nine times with five flies of a single sex in each ampoule. Arrows indicate the lower and upper pejus temperatures.

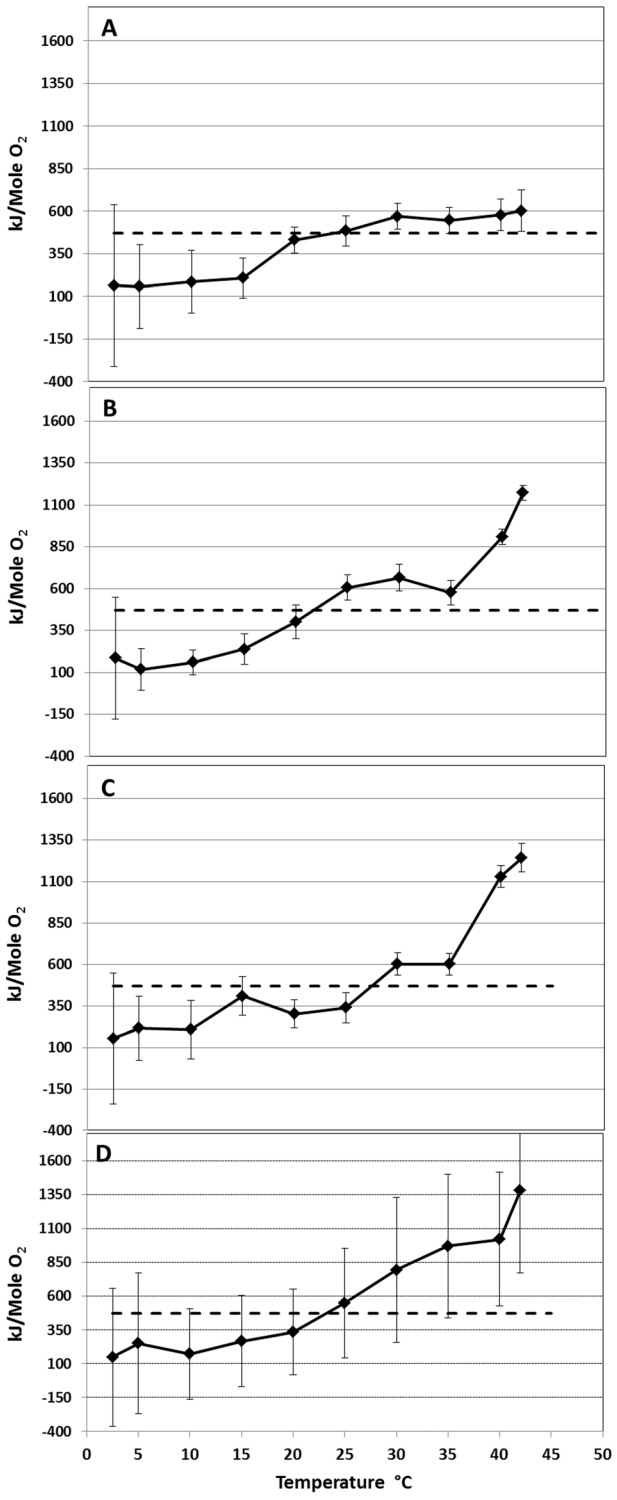

Fig. 2. Oxycaloric ratio, the ratio of metabolic hear rate to O_2 consumption rate, of (**A**) 1-, (**B**) 14-, (**C**) 21-, and (**D**) 28-d-old western cherry fruit flies calculated from data in Fig. 3. Error bars indicate standard error of the ratio. Values greater than the maximum oxycaloric ratio from Thorton's rule, 470 kJ/mol O_2 (Hansen et al. 2004) indicate anaerobic metabolism by the normal anabolic reactions of development.

Table 1. Upper and lower pejus temperatures of western cherry fruit flies in relation to age

Fly age (days)	Lower pejus temperature (°C) (±SEM)	Upper pejus temperature (°C) (±SEM)	Optimal temperature range (°C)
1 d	6.6 ± 0.26a	42.4 ± 0.08a	35.8a
7 d	9.2 ± 0.46b	40.8 ± 0.26b	31.6b
14 d	9.9 ± 0.22c	39.4 ± 0.50c	29.4c
21 d	10.5 ± 0.24d	37.8 ± 0.30d	27.2d
ΔT*	3.9 ± 2.9	4.6 ± 2.9	8.6

*ΔT indicates difference in temperature range.
Means in each column with the same letter are not statistically different.

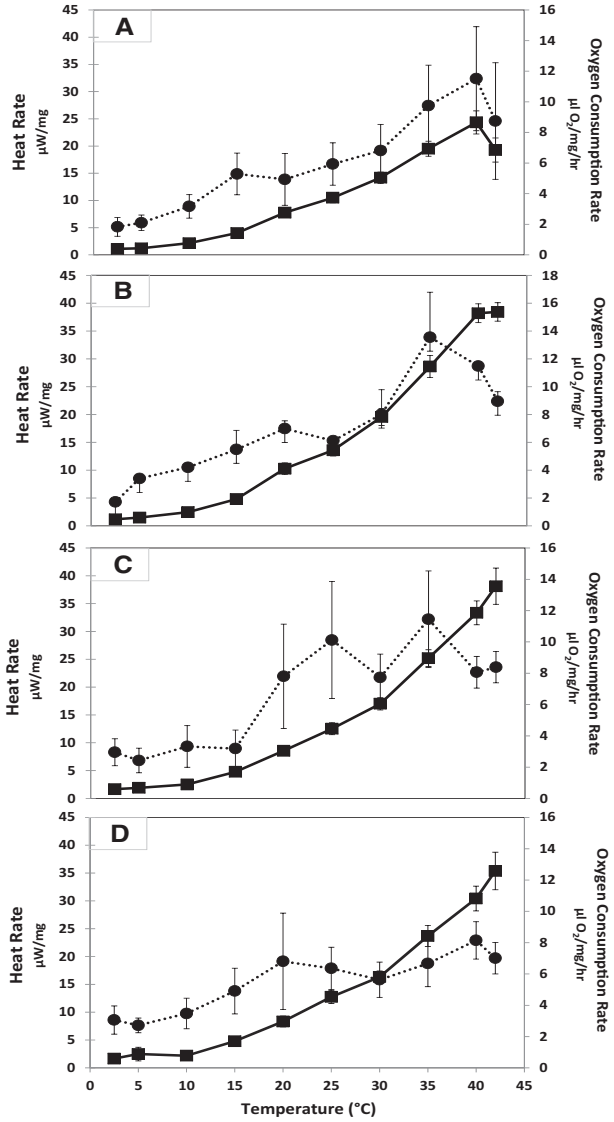

Fig. 3. Effects of various isothermal temperatures on the metabolism (-■-) and oxygen consumption rates (-●-) of (**A**) 1-, (**B**) 14-, (**C**) 21-, and (**D**) 28-d-old western cherry fruit flies. Values are an average of nine groups of flies, five flies in each ampoule.

Results and Discussion

Measurement of metabolic heat rate during a temperature scan gives an indication of the instantaneous thermal sensitivity of an organism. The lower and upper pejus temperatures were determined by identifying the temperatures where metabolism is initiated (lower pejus) and ends (upper pejus) in the individual scans (Fig. 1). The range between the lower and upper pejus temperatures decreased as the flies aged (Table 1, Fig. 1). There were significant differences between the lower pejus temperatures ($F_{3,179} = 151.507$, $P < 0.001$) as well as for the upper pejus temperature ($F_{3,179} = 188.768$, $P < 0.001$) at each age

of the flies. All lower and upper pejus temperatures were significantly different from one another as a function of fly age as determined using the Holm-Sidak method of all pairwise Multiple Comparisons Procedure ($F_{3,179} = 151.507$, all $P < 0.001$ for lower pejus, and $F_{3,179} = 188.768$, $P < 0.001$ for upper pejus). There was no difference between the lower and upper pejus temperatures as a function of sex ($F_{1,7} = 2.318$, $P = 0.225$; $F_{1,7} = 1.683$, $P = 0.285$, respectively).

There was a significant difference in the optimal temperature range of all ages of flies from one another ($F_{3,179} = 684.746$, $P < 0.001$). The 1-d-old flies had the widest range of thermal tolerance of 35.8°C whereas the most restricted range was evident in the 21-d-old flies, a range of only 27.2°C. Reduction of the range is to be expected as a function of the loss of metabolic reserves and the summation of the effects of aging and senescence (Bowler and Terblanche 2008). This is demonstrated by comparing the oxycaloric ratios (Fig. 3) at each isothermal temperature for each age of WCFF flies. The ratios of 1-d-old flies remains close to 470 kJ/mole O_2, indicating normal aerobic metabolism (Hansen et al. 2004). The ratios of 14-d-old flies rises above Thorton's constant at 25°C, and then deviated significantly at temperatures of 40 and 45°C, indicating anaerobic metabolism (Hansen et al. 2004). A similar deviation from aerobic metabolism was observed in 21-d-old flies (Fig. 3C). The oxycaloric ratio in 28-d-old flies deviated from Thorton's constant at temperatures of 30°C and above. It is interesting to note that the standard error of the oxycaloric ratios are the largest at the lowest temperatures for 1 through 21-d-old flies at temperatures at or below 15°C, indicating variation in metabolism of individuals at these lower temperatures (Fig. 3A–C). Also, the standard errors of the oxycaloric ratios for 28-d-old flies at all temperatures was the largest as compared with the other ages of flies (Fig. 3D). This large variation most likely is a function of differences in metabolism in individuals as they age and become more variable in their metabolic responses to temperatures.

The large rise in the heat rate observed around 45°C for all age groups (Fig. 1), is caused by the denaturation of organelles, proteins, and unregulated oxidation of organic compounds (Neven et al. 2014). Similar bursts have been reported for *Cydia pomonella* (L.) (Neven et al. 2014), *Drosophila melanogaster* (Meigen) (Lighton 2007), and *Tenebrio molitor* (L.) (Stevens 2010, Vorhees and Bradley 2012).

The measurement of metabolic heat rate at static, isothermal temperatures gives an indication of the range of temperatures to which an organism is acclimatized (Fig. 2A–D). The isothermal heat rates indicated that all flies could survive exposure to 40°C for at least 20 min, and that metabolism was greatly reduced, with a concomitant reduction in oxygen consumption rate, at 40–42°C. Both the 14- and 21-d-old flies exhibited a reduction of oxygen consumption at 35°C (Fig. 2B and C). The 28-d-old flies exhibited less of an increase in oxygen consumption between 25 and 40°C as compared with the other age groups (Fig. 2D). All flies exhibited a heat rate and oxygen consumption rate of zero when exposed to 45 and 50°C (data not shown), which indicates the upper critical thermal limit of the flies.

Reported longevity of western cherry fruit fly in the field is between 31 to 35 d (Yee 2003b; Yee and Chapman 2009). It has been observed that the flies seek out cooler microclimates during the hotter part of the day (Yee 2002) which may provide some protection from the extremely high afternoon temperatures, 35 to 40°C, often experienced within the fly's native range. However, it is likely that environments consisting of fewer cooler microclimates may be less advantageous to western cherry fruit fly colonization.

There is more information on the effects of temperatures on the survival and phenology of diapausing pupae of western cherry fruit fly than other life stages (AliNiazee 1975; van Kirk and AliNiazee 1981; Stark and AliNiazee 1982). There is one report on the effects of high temperatures on the immature stages, eggs through third instars, infesting sweet cherries (Neven and Rehfield-Ray 2006). There are no reports on the effects of low temperatures on the eggs and larvae of this pest.

The current models developed for western cherry fruit fly (Kumar et al. 2014a,b) used published upper and lower temperature tolerance data for diapausing pupae. Kumar et al. (2014b) used temperature index values (CLIMEX TI) of 5°C for the lower optimum temperature threshold (CLIMEX DV1) and 28°C for the upper temperature threshold (CLIMEX DV3). Given that, the thermal tolerance of adult flies fits well within the model developed based on the phenology of the diapausing pupae. However, it appears that flies can withstand slightly higher temperatures than diapausing pupae, based on other publications (Frick et al. 1954; Stark and AliNiazee 1982; van Kirk and AliNiazee 1982; Jones et al. 1991; Song et al. 2003).

These data indicate that aging of flies has an impact of thermal capacity and may influence the ability of flies to occupy climates where average daily temperatures remain above 35°C for most of the day. Field research indicates that the optimal time for western cherry fruit flies to mate and oviposit is in the mornings (Yee 2002). Climates that experience high morning temperatures may restrict the mating and ovipositon period, and influence the ability of the flies to establish and spread.

Further research is needed to determine the long-term effects of elevated temperatures on western cherry fruit fly longevity and fecundity as well as the influence of humidity levels on fly thermotolerance.

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