Field body temperature and thermal preference of the big-headed turtle *Platysternon megacephalum*

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Abstract The big-headed turtle *Platysternon megacephalum* is a stream-dwelling species whose ecology is poorly known. We carried out field and laboratory investigations to determine field body temperatures and thermal preference of this species. In the field, the body temperatures of the turtles conformed to the water temperature, with little diel variation in either summer or autumn. Over the diel cycle, the mean body temperatures ranged from 20.8°C to 22.2°C in summer and from 19.3°C to 21.2°C in autumn; the highest body temperatures ranged from 22.1°C to 25.0°C in summer and from 20.6°C to 23.8°C in autumn. In the laboratory, the preferred body temperature (T_p) was 25.3°C. Food intake was maximized at 24.0°C, whereas locomotor performance peaked at 30.0°C. Consequently, T_p was closer to the thermal optimum for food intake than for locomotion. Therefore, this freshwater turtle has relative low field body temperatures corresponding to its thermal environment. In addition, the turtle prefers low temperatures and has a low optimal temperature for food intake [*Current Zoology* 59 (5): 626–632, 2013].

Keywords Food intake, Locomotion, Preferred body temperature, Thermoregulation, Thermal sensitivity

Thermal ecology of an organism provides important implications for species distribution and population dynamics, given the overwhelming effects of body temperature on almost every aspect of organisms' lives, including behavior, metabolism, growth, and reproduction (Huey, 1982). Environmental temperatures vary temporally and spatially in nature. An organism may cope with thermal heterogeneity by means of various strategies associated with behavioural thermoregulation and physiological thermal sensitivity. Some organisms maintain nearly constant body temperatures, while others conform to environmental temperatures: stenotherms are very sensitive to temperatures, whereas eurytherms are less so (Angilletta, 2009). Endotherms precisely regulate their body temperature to a high and constant level via metabolic heating such that their functional performances can be maximized (Angilletta et al., 2010). Among ectotherms, some species conform to ambient temperatures, while others can achieve optimal temperatures for their biological functions via behavioral and physiological thermoregulations (Huey, 1982; Hertz et al., 1993). Disentangling the interactions among environment, behavior, and physiology is thus critical in understanding the thermal ecology of an organism.

Field body temperature, preferred body temperature and the temperature at which performance is maximized are important traits that have been extensively documented in a diversity of species from insects to mammals (May, 1979; Angilletta et al., 2002; Angilletta et al., 2010; Ward et al., 2010). Previous studies have recognized the importance of integrating these traits to understand the thermal ecology of organisms in their environments (e.g. Huey and Slatkin, 1976; Huey and Bennett, 1987; Angilletta et al., 2006; Angilletta, 2009). However, these studies mainly focus on squamates from relatively open habitats where solar radiation provides ample opportunities for basking (e.g. Huey and Kingsolver, 1989; Ji et al., 1996; Du et al., 2000; Zhang and Ji, 2004). In contrast, some other reptiles, such as aquatic turtles, have received much less attention, and our knowledge about thermal ecology in these species remains poor (but see Manning and Grigg, 1997; Litzgus and Brooks, 2000; Carriere et al., 2008; Dubois et al., 2009; Bulte and Blouin-Demers, 2010; Fitzgerald and Nelson, 2011). More importantly, turtles have different ecological traits from lizards and snakes. Aquatic turtles face higher rates of heat loss by conduction than do terrestrial species (Ernst and Barbour, 1989; Fitz-

gerald and Nelson, 2011). This may have driven aquatic turtles to evolve different strategies of behavioral and physiological thermoregulation from those adopted by lizards and snakes. Furthermore, turtles are long-lived, iteroparous organisms, with fitness more closely related to nutrient acquisition than to locomotion (Dubois et al., 2009). Our understanding of thermoregulation and evolutionary thermal physiology in reptiles, which is largely based on the relationship between thermoregulatory behavior and thermal sensitivity of locomotion in lizards and snakes (see review by Angilletta et al., 2002), may not be relevant to thermal ecology of turtles. Therefore, freshwater turtles provide us with an opportunity to understand thermal ecology of aquatic reptiles that could differ significantly from what we know from terrestrial species.

In this study, we measured field body temperature and thermal preference of the big-headed turtle *Platysternon megacephalum*, whose ecology is poorly known. First, a radio telemetry study was conducted in summer and autumn to determine field body temperatures and the relationship between body temperatures and ambient water temperatures. Second, we determined preferred body temperatures and thermal sensitivity of locomotion and food intake in the laboratory. We anticipated that: (1) this stream-dwelling turtle would conform to the ambient temperatures owing to low availability of heat sources in mountain streams with a dense canopy; and (2) the turtles would have low field and preferred body temperatures as well as low optimal temperatures for functional performance, corresponding to the low water temperatures of the streams in which they live (Shen et al., 2010).

1 Material and Methods

1.1 Study species

The big-headed turtle, a small freshwater turtle (up to 160 mm carapace length), is distributed throughout southern China, Laos, Myanmar, Thailand, and Vietnam (Ernst and Barbour, 1989). This species is largely nocturnal, hides beneath rocks or gravel in mountain streams during the day (de Bruin and Artner, 1999). Translocated turtles have short distances of daily movement and rarely use terrestrial habitats (<100 m) (Shen et al., 2010). However, little is known about the thermal ecology of this species.

1.2 Field thermal biology

Our study on field thermal biology used radio telemetry and was carried out in Quzhou, Southern China

(see detailed description of location and habitat in Shen et al., 2010). In summer (from late July to early August, 2007) and autumn (from late October to early November, 2007), eight recently caught wild adult turtles (4 females and 4 males, average mass 356 g) were translocated to our study site to determine the field body temperatures of the animals. To record shell temperatures, thermochron iButton temperature loggers (DS1921, 3.12 g, MAXIM Integrated Products Ltd., USA) were attached to the center of carapace of the turtles using super glue. This technology to monitor the body temperatures of free-moving animals has been verified and used in other species of freshwater turtles (e.g. Grayson and Dorcas, 2004). Thermochron temperature loggers were also set on the bank of the stream where the turtles lived (including dense vegetation, scarce vegetation and open field) to record ambient temperatures and at 10 cm below the water surface to record the water temperatures (the water is shallow in the stream, with a depth <35 cm in most places). To verify the relationship between shell temperature and core body temperature, we located six turtles during the telemetry study and measured their cloacal temperatures and the temperature of the substrate (water or earth) where the turtle was found in each season using a DM6801A electronic thermometer (±0.1°C, Shengzhen Meter Instruments, Shengzhen, China).

1.3 Thermal preference

Preferred body temperatures were determined in a 200×60×30 cm metal terrarium, at the bottom of which was 10-mm sand substrate and 50-mm-deep water. The terrarium was kept in a temperature-controlled room at 15°C. Heating mats were used to heat one end of the terrarium such that a thermal gradient ranging from 16 to 36°C was created and maintained through the experiment. A total of 24 juvenile turtles (average weight 105 g) were used in this test. We introduced one turtle each time from the cool side of the terrarium at 08:00 and measured body temperatures (cloacae, T_b) at 21:00 using the DM6801A electronic thermometer. Each turtle was measured twice, and the mean of the two readings was used as the preferred body temperature of the turtle.

1.4 Thermal sensitivity of food intake and locomotion

The effects of temperature on food intake of 10 turtles (average 260 g) were examined at five temperatures (20, 22, 24, 26, and 28°C). The animals were housed individually in a 30 × 50 cm (diameter × height) bucket with 2 cm deep water. The photoperiod of the tempera-

ture-controlled room was set at 12 h light, 12 h dark. Fish meat *Hypophthalmichthys molitrix* was provided ad libitum. The animals were kept at each test temperature for two weeks before we initiated each trial, which lasted 25 days. Pre-weighed fish meat was provided to each animal at 08:00 each day; the residual food was collected 2 hours later.

The thermal dependence of locomotion (swimming capacity) of 14 recently caught wild turtles (average 116 g) was tested at 20, 22.5, 25, 27.5 30, 32.5, and 34°C in a random order. The turtles were acclimated to the test temperature for 2 h; they were then chased along a 1.5-m-long straight racetrack filled with 50-mm-deep water to assess swimming capacity. Each turtle was tested twice at each temperature, with a half-hour resting period between trials. The swimming capacity of the turtles was recorded with a Panasonic DSC-F717 digital video camera, and the fastest swimming speed over 25-cm intervals was later scored from videotape replays.

1.5 Data analysis

We used the software package STATISTICS 6.0 to analyze data. The thermal performance breadth of food intake and locomotion was calculated as the temperature range at which 80% of the maximum performance was expressed (TPB_{80}, Van Berkum, 1986). We used linear regression to determine the relationship between cloacal temperature and shell or substrate temperature, and the regression equation of the relationship between cloacal temperature and shell temperature in each season was used to correct the shell temperatures to body (cloacal) temperatures. One-way ANOVAs were used to compare the body temperatures of turtles and environmental (both land surface and water) temperatures. All means are presented $\pm SE$, and alpha was set at 0.05.

2 Results

2.1 Ambient and body temperatures

In summer and autumn, cloacal temperatures of the turtles were closely related to substrate (mainly water, 92% of the records) temperatures as well as shell temperatures (Fig. 1). The cloacal temperatures were almost identical to substrate temperatures, and thus the correlation coefficients of regression were close to 1 (Fig. 1A). Compared with substrate temperatures, shell temperatures were less strongly related to cloacal temperatures (Fig. 1B).

During the daytime (from 08:00 to 18:00), the mean body temperatures of the turtles did not differ from water temperatures in the summer ($F_{1, 20} = 3.55$; $P = 0.08$)

and autumn ($F_{1, 20} = 0.03$; $P = 0.85$) (Fig. 2). The highest body temperatures were higher than the water temperature in summer ($F_{1, 20} = 14.94$; $P < 0.001$), but not in autumn ($F_{1, 20} = 2.70$; $P = 0.12$) (Fig. 2).

The mean land surface temperatures showed dramatic diel variation, ranging from 22.2°C to 34.1°C in summer and from 18.5 °C to 27.1°C in autumn. In contrast, diel variation in the mean water and body temperatures of the turtles was much lower than in the land temperatures. The mean water temperatures ranged from 20.4°C to 22.0°C within a day in summer, and from 19.1°C to 21.3°C in autumn. Similarly, the mean body temperatures ranged from 20.8°C to 22.2°C in summer and from 19.3°C to 21.2°C in autumn; the highest body temperatures ranged from 22.1°C to 25.0°C in summer and from 20.6°C to 23.8°C in autumn (Fig. 2).
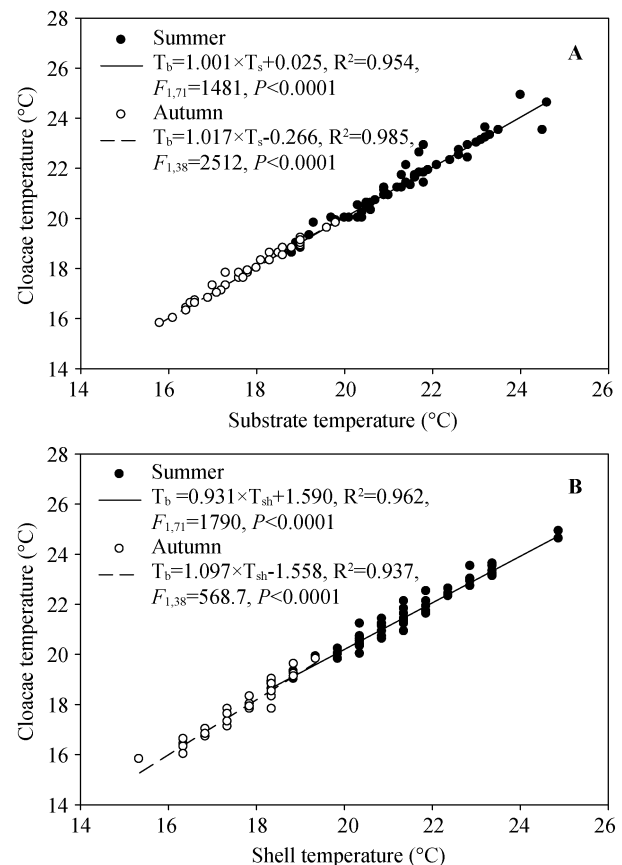

Fig. 1 The relationship between cloacal temperature (T_b) of the turtles and shell temperature (T_{sh}) and substrate temperature (T_s)

The relationships were determined by simple regressions and are shown as equations on the graphs. T_b and T_s were recorded using a digital thermometer when the turtle was located in the telemetry study; T_s was the temperature of the water or the land where the turtle was located. T_{sh} was recorded automatically by miniature data-loggers attached to the carapace of the turtles.

2.2 Thermal preference and thermal sensitivity of food intake and locomotion

The body temperatures of turtles ranged from 21.2 – 28.6°C in the thermal gradient (Fig. 3). The preferred body temperature (mean body temperature) was 25.3 ± 0.4°C. Temperature affected food intake of the turtle, with food intake achieving the highest value at 24.0°C, and declining at temperatures greater than 24.0°C ($F_{4,36}$ = 27.67; $P < 0.0001$) (Fig. 4A). The swimming capacity of turtles was dependent on temperature ($F_{6,78}$ = 4.44; $P < 0.001$), with swimming speed peaking at 30.0°C (Fig. 4B). The thermal performance breadth (TPB$_{80}$) was from 23.0 – 26.0°C for food intake, but from 27.5°C to 33.0°C for locomotion.

3 Discussion

The big-headed turtle lives in mountain streams with low water temperatures (mean temperatures range from 19.1°C to 22.0°C, Fig. 1), and shows a suite of traits corresponding to the low environmental temperatures. First, body temperatures in the field largely conformed to the water temperatures of the streams in which the turtles live, probably owing to unavailability of high environmental temperatures or the high cost of thermoregulation in a stream with dense vegetation cover. Second, the turtle preferred low body temperature that

matched the optimal temperature for food intake. Overall, the big-headed turtle has lower field body temperatures and preferred body temperatures than other aquatic turtles (Table 1).

Terrestrial ectotherms may precisely regulate their body temperatures by behavioral thermoregulation (e.g., basking, shuttling among habitats) (May, 1979; Avery, 1982). In contrast, aquatic ectotherms experience a twofold higher rate of heat transfer in the water than on land, which severely constrains their thermoregulatory capabilities when they are in the water (Fitzgerald and Nelson, 2011). Living in the water, with less opportunity for thermoregulation, aquatic turtles may develop different strategies to cope with their thermal environments: (1) most species may elevate their body temperatures by behavioral thermoregulation, such as basking [e.g., *Chrysemys picta* (Grayson and Dorcas, 2004)] and selecting a warmer microhabitat, i.e., aquatic basking [e.g., *Macroclemys temminckii* (Fitzgerald and Nelson, 2011)]; some species with a large body size may also maintain body temperatures higher than the water temperature through thermal inertia in combination with increasing heat gain behaviorally and physiologically [e.g. *Dermochelys coriacea* (Bostrom et al., 2010)]; (2) some other species simply conform to the water temperature in a warm, tropical environment [e.g.,
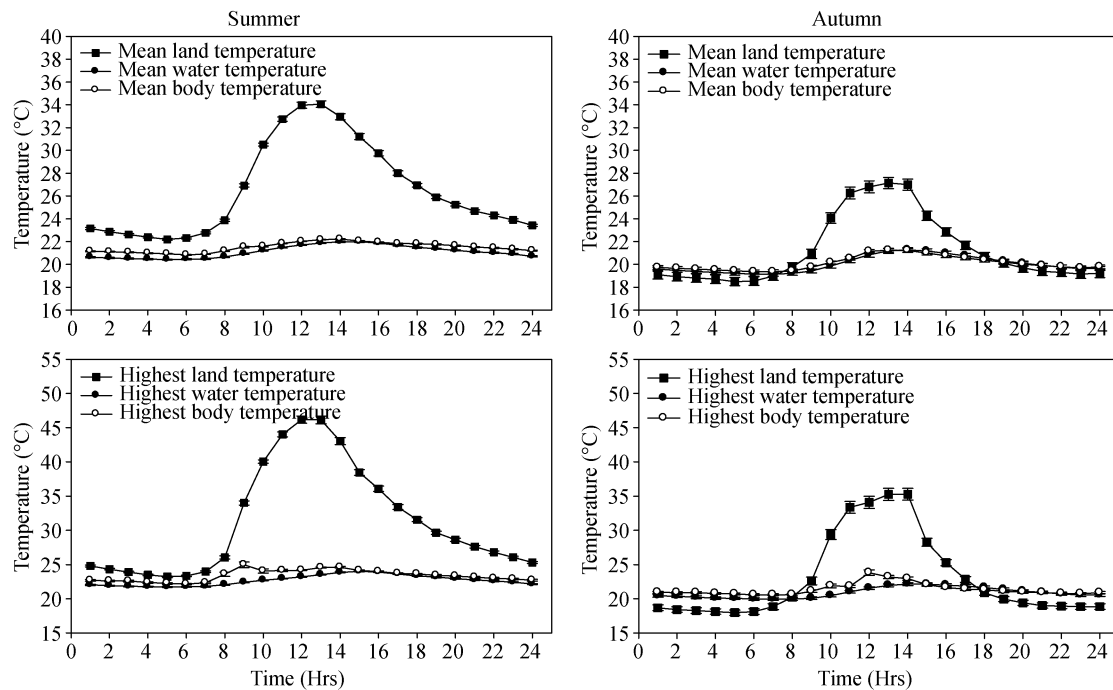

Fig. 2 Diel variation in land surface temperature, water temperature, and body temperature of the turtles *Platysternon megacephalum* in summer and autumn

The temperatures were recorded by miniature data-loggers from 23 July to 5 August 2007 in summer and from 28 September to 13 October 2007 in autumn. Data (ambient and body temperatures) are shown as means and associated standard errors on eight turtles and random sites.
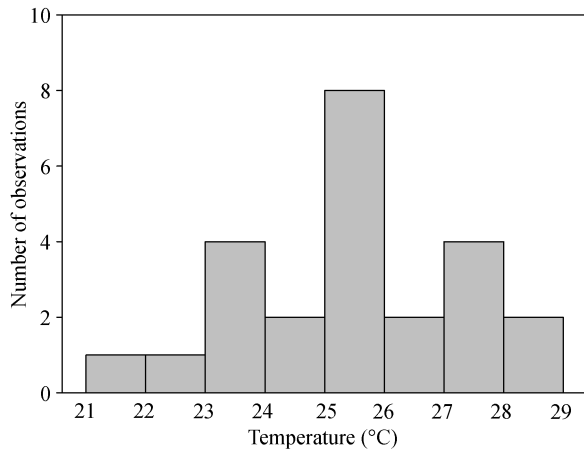
Fig. 3   The distribution of preferred body temperatures in *Platysternon megacephalum*

The body temperatures of 24 juvenile turtles were determined in a thermal gradient ranging from 16 to 36°C.

Hydromedusa maximiliani (Souza and Martins, 2006)]. Although rock patches exposed to the sun (with high daytime temperatures, Fig. 2) are available in the habitat, translocated big-headed turtles rarely use these sites for basking (Shen et al., 2010). Instead, this turtle is largely nocturnal and stays under rocks in the stream during the day, with occasional appearances on land for the purpose of reproduction (Shen et al., 2010). Aquatic basking is also unlikely to occur in big-headed turtles, as they inhabit fast-flowing shallow streams with relatively uniform water temperature. These factors largely constrain the availability for behavioral thermoregulation in this species. Consequently, the body temperatures of turtles relate to water rather than air temperatures and they are likely thermoconformers.

The thermal coadaptation theory predicts that long-lived species in environments with a high cost of ther-

Table 1   A summary of published reports on field body temperature and preferred body temperature in aquatic and semi-aquatic turtles

Species	Field body temperature (°C)	Preferred body temperature (°C)	Sources
Chelydridae			
Chelydra serpentina	22.7 (*SD*=2.8) July to August	27–30 (hatchlings) 27–33 (yearlings)	Brown et al., 1990; Bury et al., 2000.
Macroclemys temminckii	19.96 (12.21–27.76) July to February	—	Fitzgerald and Nelson, 2011.
Platysternidae			
Platysternon megacephalum	19.3–22.2 July to October	25.3 (juveniles)	This study
Emydidae			
Chrysemys picta	25–32 basking temperature	34 (juveniles)	Grayson and Dorcas, 2004; Tamplin and Cyr, 2011.
Glyptemys insculpta	23.2 (*SD*=3.9) 15–30 basking temperature	30 (juveniles)	Ernst, 1986; Tamplin, 2009.
Pseudemys nelsoni	—	30 (hatchlings)	Nebeker and Bury, 2000.
Terrapene ornata	28.0 (15.3–35.3)	28.3 (fasted) 29.8 (recently fed)	Legler, 1960; Gatten, 1974.
Trachemys scripta	27.2–38.0	30 (hatchlings) 30–33 (yearlings)	Moll and Legler, 1971; Bury et al., 2000.
Geoemydidae			
Ocadia sinensis	—	25.4–29.2 (juveniles)	Pan et al., 2003.
Trionychidae			
Apalone spinifera	—	30 (juveniles)	Feltz and Tamplin, 2007.
Pelodiscus sinensis	—	30.3 (juveniles)	Sun et al., 2002.
Chelidae			
Chelodina longicollis	March: 24.4 (*SE*=0.21) May: 20.16 (*SE*=0.33)	—	Seebacher et al., 2004.

moregulation are likely develop into specialists (Huey and Bennett, 1987; Angilletta et al., 2006). Big-headed turtles had a relatively low preferred body temperature (25.3°C) in response to the low temperatures they experienced in the stream. In addition, the optimal temperature for food intake was 24.0°C, and the food conversion coefficient and growth rate of juvenile *P. megacephalum* was maximized at 23.2°C and 23.9°C, respectively (Zhang et al., 2009). These results suggest that the turtle is a specialist for low temperatures in terms of thermal sensitivity of food assimilation and growth. The preferred body temperature of this species matches the thermal optima of food assimilation and growth (Fig.4A, Zhang et al., 2009), but not the thermal optimum for locomotion (Fig. 4B). This is probably because the optimal temperature of food assimilation and growth rate evolves more readily than that of locomotion (Angilletta et al., 2002). For example, while ectothermic vertebrates from high latitudes grow faster at low temperature than those from low latitudes at the same tempera-

ture (e.g. Bronikowski, 2000; Jonassen et al., 2000; Imsland et al., 2001), the evolution of thermal sensitivity of locomotion is relative conserved in a diversity of species (e.g. Johnalder et al., 1989; Van Damme et al., 1989; Navas, 1996).

Our results suggest that *P. megacephalum* has low body temperatures that conform to the water temperatures of the mountain streams where the turtle lives. Corresponding to the low body temperature, the turtle also has low preferred body temperatures and a low optimal temperature for food intake. In future studies, it would be of great interest to identify the constraints of and the adaptation to low environmental temperatures in this species.

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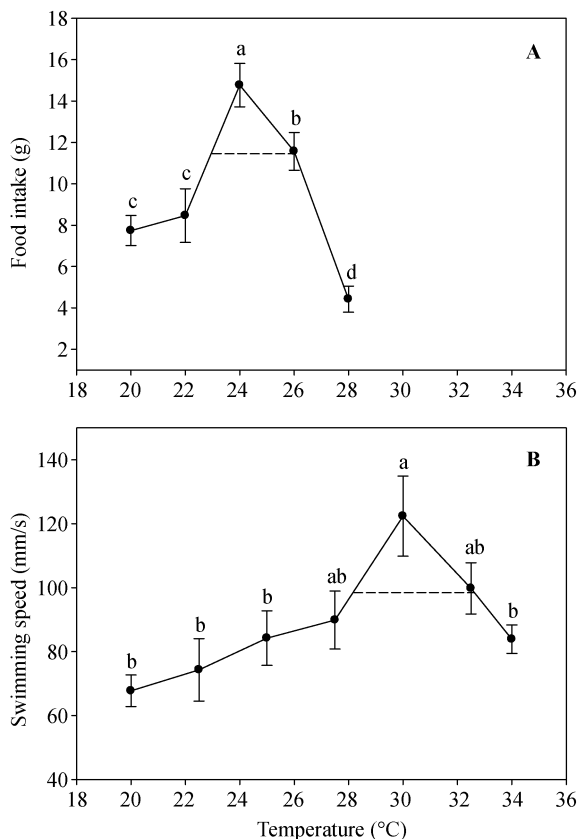

Fig. 4   Thermal sensitivity of food intake (A) and swimming capacity (B) in *Platysternon megacephalum*

Data are shown as means and associated standard errors. Means with different letters above the error bars are statistically different (Tukey's test). Sample size is 10 for food intake and 14 for swimming capacity. The dash lines indicate thermal performance breadth (TPB$_{80}$).

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