Thermal Reaction Norms of Locomotor Performance in Lacertid Lizards of the Genus *Takydromus*

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Abstract: Thermal reaction norms of sprint speed were examined in three lacertid lizard species (*Takydromus tachydromoides*, *T. smaragdinus*, and *T. dorsalis*). We found inter- and intraspecific variations in maximum sprint speed, optimal body temperature, and thermal performance breadth for the best sprints. The thermal performance breadth of *T. smaragdinus* was broader than that of *T. tachydromoides* or *T. dorsalis*, whereas *T. dorsalis* sprinted faster than the others. In *T. smaragdinus*, individuals with narrower performance breadths run faster within their thermal range of expertise. There were "specialist" individuals of which performance depended heavily on high temperatures, as well as "generalist" individuals that performed well over a broad range of temperatures even within a single population. We discussed that the spatiotemporal instability of habitats might favor more than one type of thermal reaction norm of sprint performance, and this phenomenon may be driven by specialist–generalist trade-offs.

Key words: Heterogeneous landscape; Individual specialization; Individual variation; Thermal sensitivities; Thermal usages

INTRODUCTION

Thermal resources can be utilized by several species and/or populations occupying different "thermal niches" in accordance with their different ecological and physiological traits (Ruibal, 1961; Ruibal and Philibosian, 1970). Thermal specialists that perform best within a narrow thermal niche should outcompete thermal generalists within the thermal range that is available or useful for specialists, whereas thermal generalists might perform better across a wider range of temperatures. Specialist-generalist trade-offs (i.e., a loss in performance over a broad range of environment conditions in exchange for an increase in performance within a certain

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range) explain this phenomenon well (Angilletta et al., 2003). The range of variation in body temperature in the wild could indicate whether a certain species is a thermal specialist or a generalist by comparing it to another species. We can also evaluate whether a species is a thermal specialist or a generalist based on performance curves drawn by the thermal reaction norms of phenotypical traits along thermal gradients (Scheiner, 1993; Schlichting and Pigliucci, 1998). Although intraspecific variation, such as inter- and intrapopulation variations, is a key material for adaptation in variable thermal environments (particularly for ectotherms, of which behavioral and physiological performances are highly dependent on ambient temperature), we do not fully understand how a species is composed of populations and individuals with various thermal properties (Artacho et al., 2013; Careau et al., 2014a, b).

Thermal reaction norms of locomotor performance have been well studied in lacertid lizards, and their performance curve has been fit to Gaussian or quadratic curves (Angilletta, 2006) (Fig. 1). The genus *Takydromus* exhibits interspecific variation in thermal performance from species of which locomotor ability depends strongly on certain temperatures (i.e., steep performance curves) to species that perform well over a broad range of temperatures (i.e., moderate performance curves) (Ji et al., 1996; Chen et al., 2003; Zhang and Ji, 2004; Huang and Tu, 2009). Although these studies suggest that specialist-generalist trade-offs might shape interspecific variation in thermal performance curves (Angilletta, 2009), whether the former species was composed of thermal specialists and the latter was composed of only thermal generalists remains unconfirmed.

In the present study, we investigated the thermal reaction norms of locomotor performance and the thermal usages of three lacertid lizards (*Takydromus tachydromoides*, *T. smaragdinus*, and *T. dorsalis*) distributed in temperate to subtropical zones. We analyzed interspecies and intrapopulation variations in
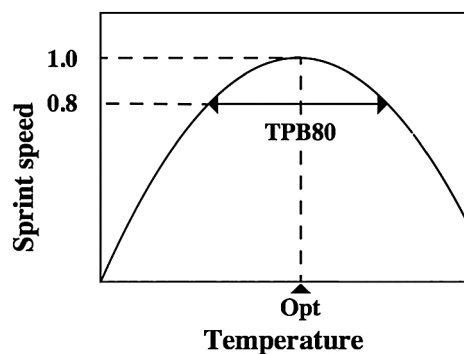

Fig. 1 A schematic figure showing optimal body temperature (Opt) and 80% thermal performance breadth (TPB80) for the best sprint in the performance curve.

locomotor performance for the first step to understand the linkage between interspecific and interindividual variations.

Materials and Methods

Animals

Takydromus tachydromoides, *T. smaragdinus*, and *T. dorsalis* are diurnal grass lizards in Japan, and their geographical distributions do not overlap (Arnold, 1997). *Takydromus tachydromoides* is broadly distributed in the northernmost area among the three species (main islands of Japan and their adjacent islands) and is found on the ground and herbaceous plants in open fields (Takenaka, 1986; Telford, 1997; Mochida et al., 2013). *Takydromus dorsalis* is semi-arboreal and is found in subtropical forests (Takenaka, 1986; Mochida et al., 2013). Its geographic range is the most southern among the three species. *Takydromus smaragdinus* inhabits the ground, herbaceous plants, and trees in the edges of forests as well as forest gaps in the subtropical islands north of the range of *T. dorsalis* (Takenaka, 1986; Mochida et al., 2013). For the sprint performance experiments, *T. tachydromoides* and *T. smaragdinus* were collected from a single field site each in Kyoto City (35°01'N, and 135°47'E) and Okinawa Island (26°45'N, 128°16'E), respec-

tively. *Takydromus dorsalis* was collected from three field sites on Iriomote Island (24°20–24'N, 123°51–54'E), but we regarded that these sites were contiguous areas. Lizards were maintained individually in plastic containers (190×120×160 mm) under a natural sunlight at an ambient temperature of 28°C in the laboratories of the University of the Ryukyus. This condition enabled the lizards to control their body temperatures by basking in the sun or hiding in a shelter in the cages. They fed on crickets the day before the sprint performance experiments.

Sprint performance experiments

The numbers of *T. tachydromoides*, *T. smaragdinus*, and *T. dorsalis* used in the sprint performance experiments were 12, 17, and 12, respectively. We did not use gravid females and small individuals (<39 mm) in which sex cannot be determined (Takenaka, 1980, 1989). The sex of each lizard was determined by the presence/absence of hemipenal bulges. We started the sprint performance experiments within four days after capture. Using a video camera (HDR-CX180; Sony Co., Ltd.), we recorded each lizard running on a racetrack with a cork sheet substratum (width 0.15 m×length 2 m) in which a graded scale at 10-cm interval was drawn to calculate their sprint speed at six different body temperatures (25°C, 27.5°C, 30°C, 32.5°C, 35°C, and 37.5°C) controlled by an incubator (MIR-153; Sanyo Co., Ltd.). Plastic containers (ca. 100×100×50 mm) were used to keep lizards in the incubator and were carried to the racetrack in insulated bags. Lizards were kept in the incubator for 30 min to ensure that their body temperature reached each experimental condition, except for the 25°C condition where we kept lizards for 45 min. An experimenter raised the cover of the container at the starting line of the racetrack. A lizard was chased by the experimenter by tapping the floor of the racetrack behind the animal to ensure that it would sprint efficiently (Angilletta et al., 2002). The experiments were carried out by two persons (KM and TS) in

the same manner to remove experimenter bias. Air temperature in the experimental room was approximately 28°C, and each experiment was finished within a few seconds after lizards were introduced into the racetrack. Lizards were raced under three temperature conditions per day and were given at least 4 h to rest between each race. We measured the sprint speed using a randomly chosen sequence of temperatures. We conducted trials during the species's typical activity periods in the field and finished all trials in two days for each individual.

We examined the sprint speed of lizards, which was defined as the speed during the fastest 50-cm interval (Zhang and Ji, 2004), under each temperature condition using video images. Maximum sprint speed was defined as the fastest sprint speed among the six temperature conditions. For the analyses of intrapopulation variation, we used relative maximum sprint speed, defined as the maximum sprint speed divided by body size as measured by snout to vent length (SVL) because SVL positively influenced sprint speed (see Results). For the evaluation of optimal body temperatures (Opt) and thermal performance breadth for best sprint, we drew performance curves for sprint speed along temperature gradients using secondary function approximation (Fig. 1) (Angilletta, 2006). For this approximation, we used the critical maximum body temperature (CTmax) at which lizards cannot move at all, implying that their performance is zero. This value was 42°C, which was taken from *T. septentrionalis* (Ji et al., 1996) and *T. sexlineatus* (Zhang and Ji, 2004), and other individuals of *T. tachydromoides* (N=11) and *T. smaragdinus* (N=3), for which CTmax was measured by the same methods of the previous study (Ji et al., 1996) (Mochida, unpublished data). The CTmax does not vary among and within *Takydromus* species (Huang and Tu, 2008). Optimal body temperature was defined as the body temperature at the peak of the performance curve, and thermal performance breadth (TPB80) was defined as the body temperature range within

TABLE 1. Interspecific variation in thermal properties of *Takydromus* species. Opt is the optimal body temperature for the best sprint performance, and TPB80 is the 80% performance breadth for the sprint. The number of *T. tachydromoides*, *T. smaragdinus*, and *T. dorsalis* used in the experiment were 12, 17, and 12, respectively. Tb and Te are field body temperatures and ambient environment temperatures, respectively. Ranges and number of samples are shown in parentheses. All data are shown as mean±SE.

Species	SVL (mm)	Maximum sprint speed (m/sec)	Opt (°C)	TPB80 (°C)	Tb (°C)	Te (°C)
T. tachydromoides	51.6±1.8	1.6±0.1	31.6±0.2	9.56±0.15	32.9±0.5 (25.3–37.1, 41)	29.7±0.5 (20.7–33.6, 41)
T. smaragdinus	48.1±1.3	1.6±0.1	31.1±0.3	10.11±0.28	31.8±0.5 (25.8–36.4, 33)	29.4±0.6 (24.1–35.5, 33)
T. dorsalis	61.1±2.4	2.4±0.2	31.2±0.4	10.09±0.25	32.1±0.3 (30.1–34.5, 11)	28.7±0.1 (27.2–29.7, 11)

which lizards run at more than 80% of sprint speed at Opt (Fig. 1) (Van Berkum, 1986).

Field body temperature

Body temperatures (Tb) of wild lizards were measured using a digital thermometer (SK-1260; Sato Keiryoki Mfg. Co., Ltd.) inserted into their cloacae in the same field sites from which the lizards were collected for the experiments. Lizards were captured and handled carefully to minimize heat exchange with human hands. Body temperatures of *T. tachydromoides* were measured during the daytime from August to October 2012 (a total of 11 days and 41 individuals), that of *T. smaragdinus* were from May to September 2012 (12 days and 33 individuals), and that of *T. dorsalis* were July and September 2013 (5 days and 11 individuals). We carried out measurements during at least 2 days in each month. We measured ambient environment temperatures (Te) in the sunshade where lizards were collected. We also recorded environment temperatures for a year (September 2012–October 2013) at one field site of *T. dorsalis* using a thermorecorder (TR-52i and TR-50U; T&D Co.) because we did not collect enough Te data of *T. dorsalis* (Table 1). We set the thermorecorder in the sunshade at the trunk of a tree where the lizards perched.

Statistics

Using information theoretic model comparisons based on the Akaike Information Criterion (AIC) in general linear models (GLMs), we examined the effects of interspecific and sexual differences on maximum sprint speed, optimal body temperature (Opt), and 80% thermal performance breadth (TPB80). We used the restricted maximum likelihood model (REML) to decompose the variances and to
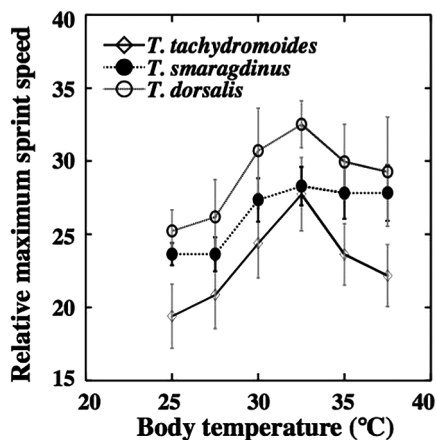

FIG. 2 Thermal sensitivity of sprint speed varies among *Takydromus* species. Relative maximum sprint speed was defined as maximum sprint speed divided by snout-vent length. Error bars indicate SE.

TABLE 2. The models that best explain the variation in thermal properties of *Takydromus* species. In models that fitted maximum sprint speed as a response variable, full and null models are also shown.

Response variables	ΔAIC	Order	Models
Maximum sprint speed	—	1	Species+SVL
	1.46	2	Species+SVL+Tail
	1.46	3	Species
	1.97	4	Species+SVL+Sex
	3.45	5	Species+Tail
	3.45	6	Full model (Species+SVL+Tail+Sex)
	21.50	15	Null model
Optimal body temperature	—	1	Null model
	2.00	2	Sex
	2.18	3	Species
	3.96	4	Full model (Species+SEX)
80% thermal performance breadth	—	1	Species
	1.23	2	Null model
	1.70	3	Full model (Species+Sex)
	3.21	4	Sex

TABLE 3. Explanatory variables contributing to variation in thermal properties of *Takydromus* species. Statistical significance of each coefficient was tested by a Wald test.

Response variables	Explanatory variables		Coeff.	SE	*T*-value	*P*-value
Maximum sprint speed	Species	if *T. dorsalis*	0.31	0.11	2.743	0.009
		if *T. smaragdinus*	0.00	0.09	0.006	0.995
	SVL		0.01	0.00	1.910	0.064
Optimal body temperature	—					
80% thermal performance breadth	Species	if *T. dorsalis*	0.07	0.04	1.847	0.073
		if *T. smaragdinus*	0.07	0.03	2.084	0.044

derive parameter estimates using Gamma error and a log-link function in the models. In the GLMs, the response variables were maximum sprint speed, Opt, and TPB80, and species and sex were the explanatory variables. We also added the effects of SVL and tail length as explanatory variables in the models in which the response variable was maximum sprint speed. Statistical analyses were performed using R software ver. 3.5.0 (R Core Development Team).

Results

Sprint speed was sensitive to body temperature in all three *Takydromus* species examined (Fig. 2). In the model that best explained the variation in maximum sprint speed, the explanatory variables were species and SVL (Table 2). Although ΔAIC is not substantial, species was selected as an explanatory variable in the best five models, and also SVL was selected in the three out of the best five mod-
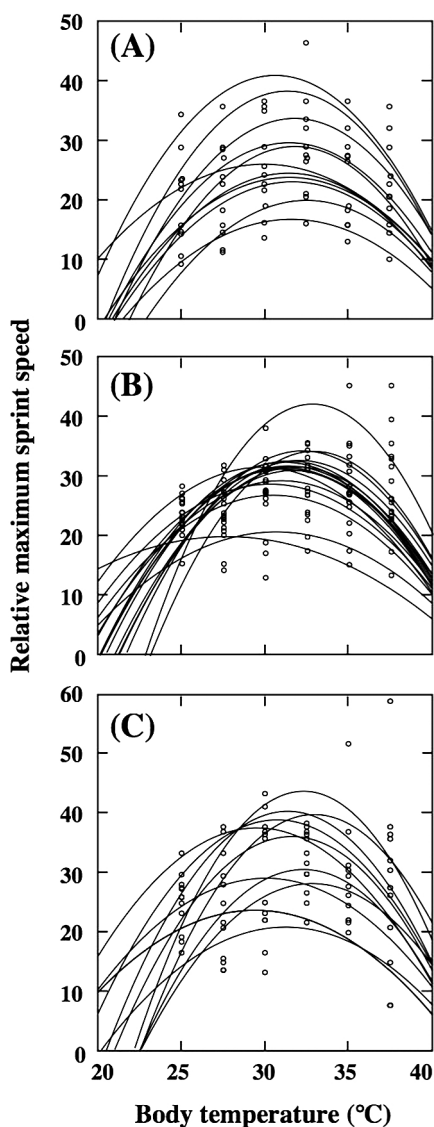
FIG. 3 Intraspecific variation in thermal performance curves in *T. tachydromoides* (A), *T. smaragdinus* (B), and *T. dorsalis* (C) drawn by secondary function approximation.

els (Table 2). *Takydromus dorsalis* sprinted faster than the other species (Fig. 2; Table 3). SVL positively influenced maximum sprint speed (although the p-value fell short of the 0.05 level), but sex difference and tail length did not (Table 3). In Opt, the null model best explained its variation (Table 2). There were

no interspecific and sexual differences in Opt. In the model that best explained the variation in TPB80, the explanatory variable was only interspecific difference, although the ΔAIC is not substantial (Table 2). *Takydromus smaragdinus* showed wider performance breadth than the other species (Table 3). Therefore, we combined data for both sexes and used relative maximum sprint speed in the following intraspecific analyses.

We did not find interspecific differences in field Tb (one-way Welch test; F=0.351, P=0.707) and Te (one-way Welch test; F=1.158, P=0.322). The thermorecorder showed that the highest temperature in the habitat of *T. dorsalis* throughout the year was 32.9°C (27 October 2012).

We drew thermal performance curves and examined partial correlations among relative maximum sprint speed, Opt, and TPB80 of each individual for each species (Fig. 3). In *T. tachydromoides*, we found a significant correlation between Opt and TPB80 (r=–0.736, P=0.010) but not between Opt and the maximum sprint speed (r=–0.258, P=0.444) and between TPB80 and the maximum sprint speed (r=0.038, P=0.911). Similarly, in *T. dorsalis*, we found a significant correlation only between Opt and TPB80 (r=–0.934, P<0.001) and not between Opt and the maximum sprint speed (r=0.355, P=0.284) and between TPB80 and the maximum sprint speed (r=0.208, P=0.540). In *T. smaragdinus*, we found significant correlations between Opt and TPB80 (r=–0.877, P<0.001) and also between Opt and the maximum sprint speed (r=0.617, P=0.011), but not between TPB80 and the maximum sprint speed (r=0.284, P=0.287) (Fig. 4). Collectively, in all three species, lizards in which Opt was higher also have narrower thermal performance breadths. The individuals with higher Opt could run faster only in *T. smaragdinus*.

DISCUSSION

Thermal environments and internal demands of physiological functions explain
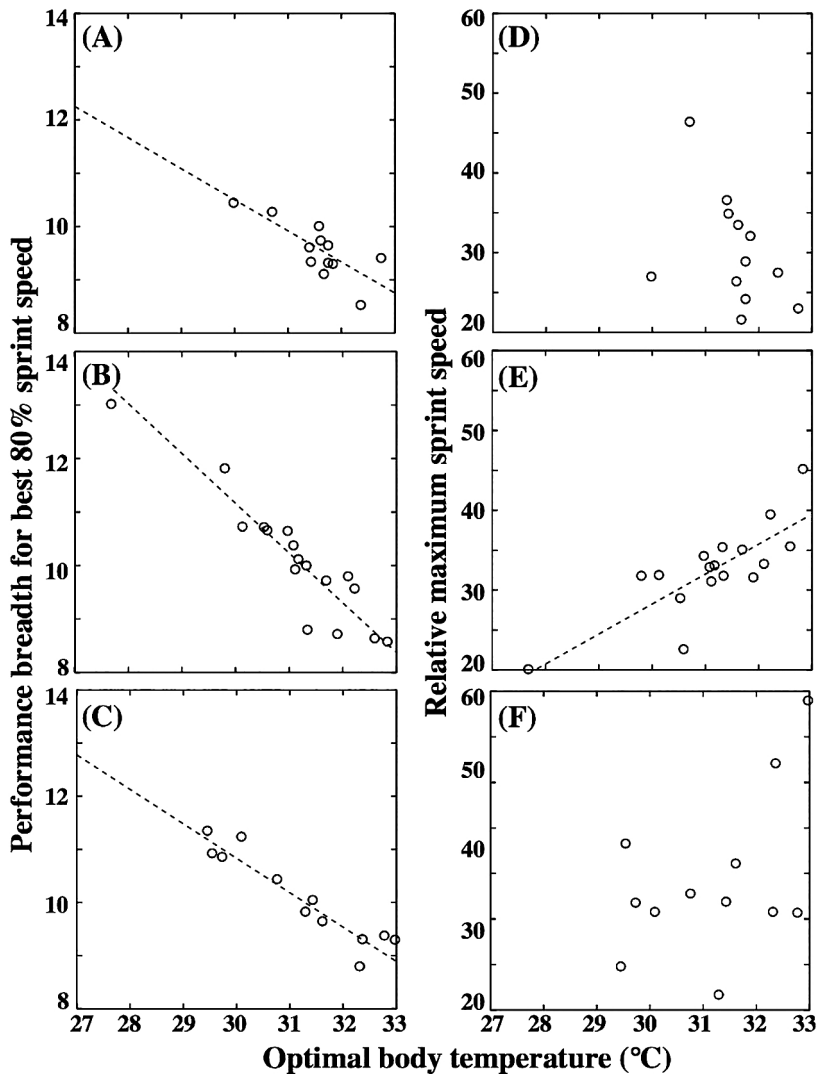
FIG. 4 Intraspecific variation in sprint speed, optimal body temperature, and thermal performance breadth for the best sprints. Optimal body temperature was negatively correlated with thermal performance breadth in *T. tachydromoides* (A), *T. smaragdinus* (B), and *T. dorsalis* (C), and it was positively correlated with relative maximum sprint speed in *T. smaragdinus* (E), but not in *T. tachydromoides* (D) and *T. dorsalis* (F).

inter- and intraspecific variations in thermal reaction norms (Angilletta, 2009). Zhang and Ji (2004) found that *T. sexlineatus* distributed in the tropics showed its optimal body temperature for sprinting (Opt) was at the high temperature range. Its thermal performance breadth is narrow, and therefore, the shape of its performance curve is steep compared with

those of species distributed in moderate temperature zones. *Takydromus wolteri*, distributed at high altitudes, shifts its Opt toward lower temperatures, and the shape of its performance curve is steep. *Takydromus sexlineatus* and *T. wolteri* are able to run faster in their Opt than other species. Thus their thermal properties are considered to adapt to the

extreme thermal environments. We collected three *Takydromus* species from temperate to subtropical zones ranging over 10 degrees of latitude, but did not find differences in Opt among species. *Takydromus dorsalis* inhabits evergreen broad-leaved forests that are fully or mostly covered by canopies, and the amount of solar radiation (the primary heat source for lizards) in this habitat is the lowest among the three *Takydromus* species (Mochida et al., 2015; Mochida, unpublished data). Te and habitat temperature measured by a thermorecorder suggested that *T. dorsalis*'s habitat is not the hottest in summer among the three species, although its geographic range is the most southern. *Takydromus smaragdinus*, which is distributed in a latitudinal area intermediate between that of the other two species, also inhabits subtropical forests; however, it chiefly inhabits the forest edges and gaps (Mochida et al., 2013). *Takydromus dorsalis* and *T. smaragdinus* might not be exposed to relatively strong solar radiation compared with *T. tachydromoides*, which live in open fields of temperate zone. Among the three *Takydromus* species that we studied, species that are distributed in more southern areas would use more woody habitats to avoid solar radiation, and therefore, there may be little difference in Te among these species. Behavioral thermoregulation, such as habitat-shifting and habitat-choice, reduces the physiological adjustment needed to compensate for changing thermal environments (Angilletta, 2009); this may be a reason for the absence of differences in Opt among the three *Takydromus* species.

A horizontal shift in Opt and change in the steepness of the thermal performance curve were detected within populations in each species (Fig. 4-A, B, and C), which are comparable to the patterns observed among species by a previous study (Zhang and Ji, 2004). Also, we found that in *T. smaragdinus*, individuals for which Opt shifts toward higher temperatures and TPB80 is narrower have higher maximum sprint speeds at their Opt (Fig. 4-B and E). The reduction of TPB80 with high

Opt might be derived from not only biological adaptation but also a mathematical artifact because we set 42°C as CTmax to calculate Opt and TPB80 in all individuals. In addition, the pattern of individual-level variation was not confirmed by repeated measurements of sprint performance. However, our results suggest that specialist-generalist trade-offs might serve to maintain individual-level variation in thermal performance curves especially for *T. smaragdinus*, which shows variation within a population similar to interspecific variation in thermal reaction norms reported by Zhang and Ji (2004). This supports the notion that thermal sensitivity and physiological performance can co-evolve within a population (Angilletta et al., 2003).

Temporal stability in thermal environments favors thermal specialists, whereas instability in thermal environments favors thermal generalists or specialists depending on the balance between among- and within-generation variations in the thermal environments (Gilchrist, 1995). In addition to the temporal fluctuation, the spatial heterogeneity of habitats might cause the adaptive landscape to have multiple peaks for thermal characters, driving polymorphism within a population (Van Tienderen, 1991). A *Takydromus smaragdinus* population might be composed of several types of thermally characterized individuals. Thermal environments of *T. smaragdinus* could often temporally change because of disruption of vegetation by typhoons, and their habitats are more spatially heterogeneous, including both scrub and forests, when compared to the other two species. Although our results for intrapopulation variation in thermal properties need further verification of the persistence of the individual traits by repeated measurements, the present study highlights the importance of individual-level analyses of thermal reaction norms and the role of the external environment on the evolution of thermal reaction norms.

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