

Conservatism of thermal preferences between parthenogenetic *Aspidoscelis cozumela* complex (Squamata: Teiidae) and their parental species

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Closely-related species can exhibit similar thermal requirements despite inhabiting different environments. Hybrid species between them can exhibit a diversity of thermal requirements, or can be similar to parental species. In this study, we investigated thermal preference and efficiency in parthenogenetic *Aspidoscelis cozumela* complex lizards (*A. cozumela*, *A. rodecki*, *A. maslini*) and their parental species (*A. angusticeps* and *A. deppii*), to determine whether thermal preferences are conservative. We found that thermal preferences are similar among species and determined by phylogenetic relationships. *Aspidoscelis deppii* (paternal species), *A. cozumela* and *A. maslini* showed similar thermal preferences, whereas *A. rodecki* was similar to the maternal species (*A. angusticeps*). These results suggest that thermal preferences of parthenogenetic lineages match with one of the parental species and are not restricted to one gender. These findings support the “frozen niche variation” hypothesis.

Key words: *Aspidoscelis cozumela* complex, conservatism, parthenogenesis, thermal preferences

INTRODUCTION

Clonal reproduction, theoretically, may present disadvantages due to a number of factors, including higher accumulation of deleterious mutations, uniformity among descendants and the restricted potential of phenotypic evolution. Thus, clonal taxa have been considered as organisms with short geological lifespans (Leslie & Vrijenhoek, 1977; Bell, 1982; Spinella & Vrijenhoek, 1982; Maynard Smith, 1986; Lynch & Gabriel, 1990). However, all-female parthenogenetic lineages which arose through hybridization of two gonochoristic species represent a widespread and viable strategy used by different taxa during extended periods (Avice, 2008). Some unisexual vertebrates form abundant populations across wide geographical distributions, inhabiting different environmental conditions (Kearney et al., 2003; Fujita & Moritz, 2009).

Environmental characteristics determine behavioural and physiological traits of organisms (Sinervo et al., 2010). Ectotherms maintain a relatively constant body temperature (*T_b*) by thermoregulatory behaviour, which allows them to perform biological activities such as foraging, feeding, growth, predator evasion and reproduction (Vitt, 1974; Avery, 1982; Bartholomew, 1982; Huey, 1982). The *T_b* of ectothermic organisms such as lizards is the result of habitat use, foraging

and activity periods interacting with environmental temperature (Huey, 1982; Adolph, 1990; Hertz, 1992; Hertz et al., 1993; Andrews, 1998; Blouin-Demers & Nadeau, 2005; Medina et al., 2009). Intrinsic factors such as mass, body length, reproductive state and phylogeny may explain variation of *T_b* in lizards. For example, some phylogenetically closely related species exhibit similar *T_b* despite inhabiting different environments (Bogert, 1949; Schall, 1977; Rocha & Vrcibradic, 1996; Andrews, 1998). According to these studies, the thermal preferences of ectothermic species is evolutionary conserved (Adolph, 1990; Andrews, 1998; Menezes & Rocha, 2011).

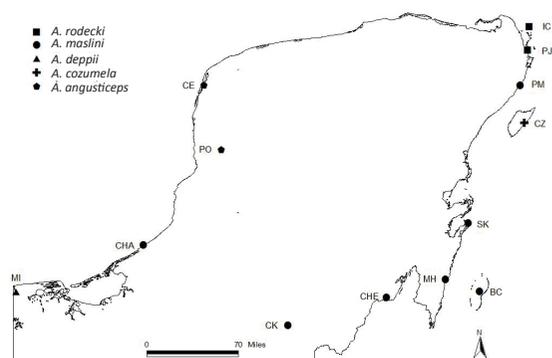


Fig. 1. Study populations of the *A. cozumela* complex and parental species.

There are many reasons to expect that clonal organisms differ phenotypically from their parental species (Lynch, 1984; Kearney & Shine, 2004a). Parthenogenetic organisms are characterized by high heterozygosity, which may lead more broadly tolerant phenotypes, and multiple hybrid origins can provide a further source of clonal diversity (Kearney & Shine, 2004b). Parthenogenetic species provide an opportunity to evaluate the thermal conservatism in ectothermic species. The ability of parthenogenetic species to coexist with sexual species has been encapsulated in the Frozen Niche Variation (FNV) hypothesis. Because parthenogenetic species arise through hybridization between two sexual species, each clone has “frozen” a part of the genome from their ancestors, expressing similar ecological and/or physiological requirements (Vrijenhoek, 1979, 1984; Paulissen, 1988; Parker et al., 1989). Clones may therefore represent the genetic and phenotypic diversity of parental species (Vrijenhoek, 1984; Kearney et al., 2003). Interclonal selection may further favour local adaptation among clones with different physiological requirements or resource use (Vrijenhoek, 1984; Pagano et al., 2008). However, the hypothesis of thermal conservatism in selected temperature (*T_{sel}*) is not supported by some studies (Huey & Slatkin, 1976; Fuentes & Jaksic, 1979). The General Purposes Genotypes (GPG) hypothesis proposes that a hybrid genotype fits a broad ecological niche, and exhibits similar levels of fitness in parental and intermediate niches. These could be explained by heterosis resulting from hybridization, through the evolution of polyploidy, or through selection for generalist clones (Kearney et al., 2003). Consequently, clonal diversity declines and only the most generally adapted clones persist, causing divergence between phenotypes of parthenogenetic and gonochorist species (Pagano et al., 2008). However, clonal organisms may exhibit high levels of physiological variation, which provides an advantage when faced with environmental changes (Parker, 1979; Lynch, 1984; Paulissen, 1988). Both hypotheses predict a hybrid advantage similar to the general hybrid vigour scenario (Bulger & Schultz, 1979; Dohm et al., 1998).

Previous studies on lizards of the family Teiidae revealed their ecology is influenced by environmental conditions (Pianka, 1970; Schall, 1977; Bergallo & Rocha, 1993; Magnusson, 1993; Menezes et al., 2000; Menezes & Rocha, 2011). Therefore, the study of parthenogenetic and parental gonochoristic species which inhabit different environments is an ideal model to determine how thermal preferences are influenced by ecological conditions and phylogenetic constraints. Lizards of the genus *Aspidoscelis* are actively foraging and oviparous, and typically characterized by high *T_b* between 36 and 41°C (Sievert & Paulissen, 1996; Pianka & Vitt, 2003; Winne & Keck, 2004; Woolrich-Piña et al., 2011). One third of all species of this genus are parthenogenetic (Wright, 1993; Reeder et al., 2002). The parthenogenetic *A. cozumela* complex originated from two independent hybridization events (*A. maslini* and *A. rodecki*) between phylogenetically separated sexually reproducing species: *A. angusticeps* (maternal species) and *A. deppii* (Fritts, 1969; Moritz et al., 1992; Reeder et al., 2002). The third parthenogenetic species from this complex (*A. cozumela*) was proposed by Taylor & Cooley (1995) based on morphological variation. *Aspidoscelis cozumela* could have arisen through three centromeric chromosome fissions of a female *A. maslini* (Manríquez-Morán et al., 2000). Cytological, morphological, colour-based and karyotypic evidence further support the species status (McCoy & Maslin, 1962; Fritts, 1969; Moritz et al., 1992; Hernández-Gallegos et al., 1998; Manríquez-Morán et al., 2000; Taylor et al., 2005; Manríquez-Morán & Méndez-de la Cruz, 2008). The parthenogenetic *A. cozumela* complex inhabits mainly halophytic vegetation along beaches of the Yucatán peninsula. *Aspidoscelis angusticeps* is found in continental and coastal areas of the peninsula, whereas *A. deppii* is widespread in southwestern Mexico and Central America; in the Yucatán peninsula it inhabits a restricted area along the coast of the Gulf of Mexico as well as southern areas (Wright, 1993; Lee, 1996; Fig. 1).

The *A. cozumela* complex is characterized by low interspecific genetic variation (Moritz et al., 1992; Manríquez-Morán et al., 2000; Manríquez-Morán, 2002;

Table 1. Study populations and modes of reproduction.

Species	Site	Population	Code	Reproduction
<i>Aspidoscelis maslini</i>	Campeche	Champotón	CHA	Parthenogenesis
	Campeche	Calakmul	CK	Parthenogenesis
	Quintana Roo	Mahahual	MH	Parthenogenesis
	Quintana Roo	Banco Chinchorro	BC	Parthenogenesis
	Quintana Roo	Chetumal	CHE	Parthenogenesis
	Quintana Roo	Puerto Morelos	PM	Parthenogenesis
	Quintana Roo	Sian Kaan	SK	Parthenogenesis
<i>Aspidoscelis rodecki</i>	Quintana Roo	Isla Contoy	IC	Parthenogenesis
	Quintana Roo	Puerto Juárez	PJ	Parthenogenesis
<i>Aspidoscelis cozumela</i>	Quintana Roo	Isla Cozumel	CZ	Parthenogenesis
<i>Aspidoscelis angusticeps</i>	Yucatán	Celestun	CE	Gonochorist
	Campeche	Pomuch	PO	Gonochorist
<i>Aspidoscelis deppii</i>	Tabasco	Miramar	MI	Gonochorist

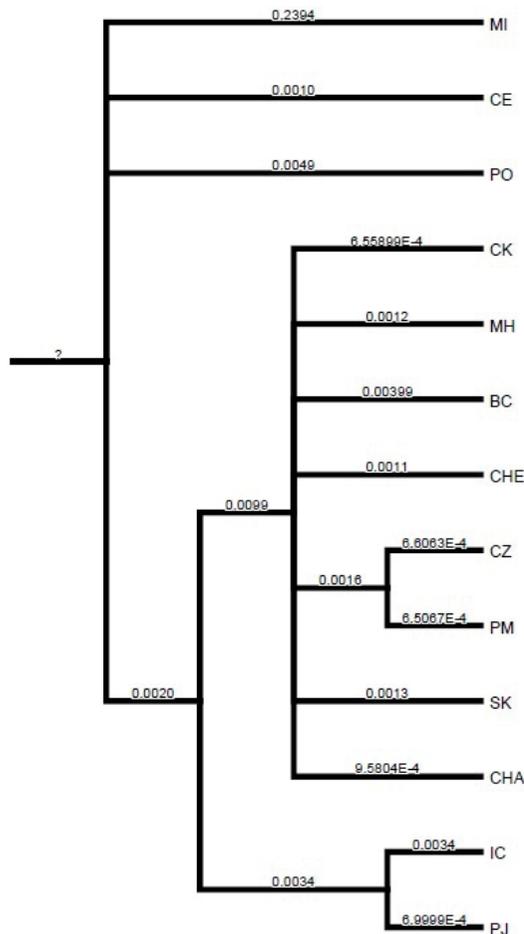


Fig. 2. Phylogeny of the study populations.

Hernández-Gallegos et al., 2003). Parthenogenetic lineages and their parental species inhabit different environments, which could substantially differ from each other in thermal quality. Therefore, the *A. cozumela* complex and its parental species are ideal to test the hypothesis that thermal preferences could be evolutionary conserved. The present study addresses the relationship between the thermal environment and thermal preferences of the *A. cozumela* complex and the parental species. We conducted a phylogenetically controlled analysis to i) determine the T_b s of the parthenogenetic species of the *A. cozumela* complex and their parental species, ii) describe how thermal efficiency is affected by thermal quality of the habitat and iii) quantify the influence of the parental species' thermal preferences on clonal lineages.

MATERIALS AND METHODS

Thermal efficiency and field methods

We studied 13 populations (Table 1) over five years (2008 to 2012) during the spring and summer seasons. We sampled all populations three times over a period of five days, excepted for Pomuch (PO), Miramar (MI), and Celestun (CE) which were visited for a 10 day period. Most studied populations inhabit sandy beaches and dunes with halophytic vegetation, whereas three populations (Chetumal: CHE, Calakmul: CK, Pomuch: PO) were studied in rainforest environments (Lee, 1996). We

collected lizards during the activity period (1000–1700 hours) and measured T_b directly from the cloaca with a quick reading thermometer (Miller-Weber, precision 0.1°C) immediately after capture (Mathies & Andrews, 1995; Andrews et al., 1999). We also measured substrate temperature (T_s , in shaded substrates occupied by the lizard) and air temperature (T_a , in shaded areas 1 cm above the ground where the lizard was caught). To obtain operative temperatures (T_e) we used five copper models which were similar in size and shape to the lizards (Hertz et al., 1993). We connected the copper models to data loggers which registered the temperature each 15 minutes during the activity period (1000–1700 approximately) on at least 10 days (the same days during which lizards were caught) for each population. We placed the models in areas where lizards were observed foraging, to obtain the thermal characteristics of the habitat sand (direct sun), halophyte vegetation (partial shade) and under the palms or vegetation (shade). We calibrated them in the laboratory and under field conditions to confirm that the models match with thermal responses of restrained lizards under simulated and field conditions (Appendix 1).

In order to obtain selected temperatures (T_{sel}) and selected temperature intervals (T_{set}), we transported all collected lizards to a room with controlled temperature (25°C) followed by exposing them to a thermal gradient (25°C–50°C) which was generated in polycarbonate box (Appendix 2). We used T_b , T_e and T_{sel} to calculate thermoregulatory precision indexes (\bar{a}_b), habitat thermal quality (\bar{a}_e), the thermoregulatory efficiency index (E) according to the protocol of Hertz et al. (1993), and the effectiveness thermoregulation index ($B-W$) proposed by Blouin-Demers and Weatherhead (2001, see also Appendix 3). All lizards were released at their place of capture after the experiments.

Statistical analysis

We performed multiple regressions to evaluate the relationships among T_a , T_s and T_b . The species share common ancestry and cannot be regarded as statistically independent (Felsenstein, 1985). To determine whether thermal preferences vary with thermal environment or whether they are conserved, we therefore performed Pearson correlations between T_{sel} and T_b against T_e incorporating phylogenetic independent contrasts (PIC) using the module PDAP: PDTREE in MESQUITE 2.75 (Midford et al., 2005; Maddison & Maddison, 2009). Phylogenetically controlled analyses were developed based on published phylogenies (Manríquez-Morán, 2002), to which we added more populations to obtain an *ad hoc* tree (Fig. 2). We used ND4 and CytB genes to establish these phylogenetic relationships. After the PIC test we determined levels of similarity in T_b and T_{sel} . To test for differences among species we used ANOVA, and to test for differences among populations we used non-parametric Kruskal-Wallis tests followed by *post-hoc* Tukey tests. JMP® and Sigma Plot 10® were used. The significance value for all the statistical tests was $p < 0.05$ (Sokal & Rohlf, 2000); data are presented as mean ± standard error and temperature intervals.

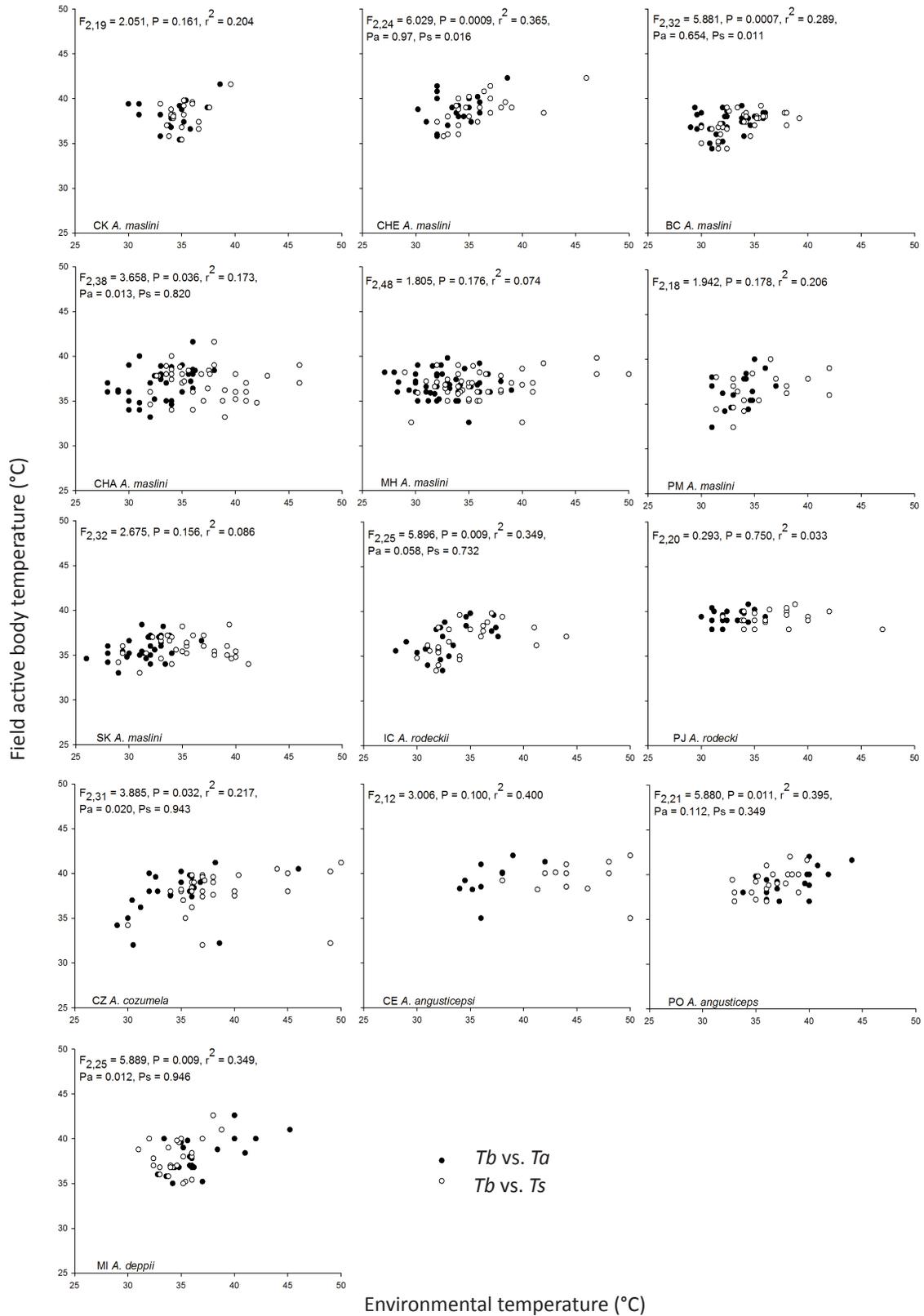


Fig. 3. Multiple regression of field body temperature (T_b) against air and substrate temperature (T_a and T_s) in separate populations.

RESULTS

The T_b of parthenogenetic and parental populations ranged from 35.7°C (SK, *A. maslini*) to 39.4°C (CE, *A. angusticeps*). The T_b of seven populations belonging to five species were determined by environmental temperature (Fig. 3), and we subsequently determined

the environmental influence variable for each population (T_a : CHE and BC; T_s : CHA, IC, CZ, MI and PO).

The PIC approach suggests that T_b and T_{sel} of parental and parthenogenetic species are not significantly correlated with T_e (Fig. 4), and that they are independent of environmental temperatures (T_b vs. T_e : $r_{11}=0.2336, p=0.442$ and T_{sel} vs. T_e : $r_{11}=0.1647, p=0.5907$).

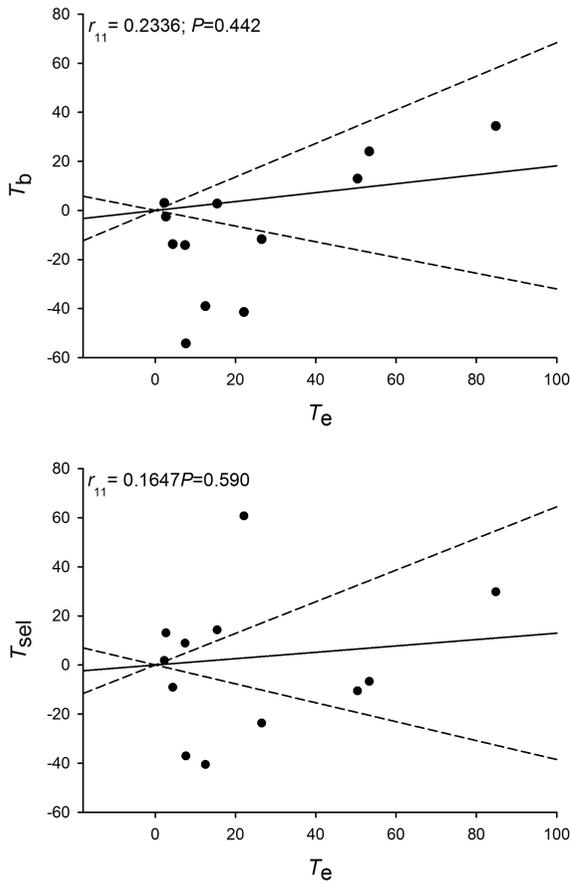


Fig. 4. Relationships between T_b and T_e , T_{sel} and T_e using phylogenetically independent contrasts.

Aspidoscelis angusticeps showed the highest mean T_b (39.30 ± 0.32 °C), which was different from all other species ($F_{351,4} = 11.736$, $p < 0.05$), followed by *A. cozumela* (38.04 ± 0.33 °C), *A. deppii* (37.94 ± 0.37 °C), *A. rodecki* (37.89 ± 0.27 °C) and *A. maslini* (37.12 ± 0.12 °C) which were not significantly different from each other (detailed data not shown). *Aspidoscelis rodecki* (37.40 ± 0.16 °C) and *A. angusticeps* (37.34 ± 0.16 °C) had the highest T_{sel} , which was significantly different ($F_{298,4} = 21.87$, $p < 0.05$) from the other three species (*A. deppii*: 35.77 ± 0.18 °C, *A. maslini*: 35.41 ± 0.08 °C, *A. cozumela*: 35.15 ± 0.21 °C).

Significant differences were found among all T_b s ($H = 114.39$, $df = 12$, $p < 0.05$). CE, PO and PJ presented the highest T_b , whereas SK, PM, MH and IC presented the lowest mean T_b . According to the post-hoc tests the populations of *A. angusticeps* (CE and PO) were not significantly different from each other, presenting the highest T_b means among all studied populations (Table 2). We found significant differences in T_b between the *A. rodecki* populations, with PJ presenting one of the highest temperatures. Also populations of *A. maslini* differed from each other, with CHE and CK being highest. The populations of *A. cozumela* and *A. deppii* were similar and close to the high temperature populations of *A. maslini* (Fig. 5).

We found significant differences in T_{sel} among populations ($H = 116.57$, $df = 12$, $p < 0.05$); T_{sel} ranged from 34.8 °C (SK) to 38.8 °C (PJ). The populations with higher thermal preference were PJ (*A. rodecki*), PO (*A.*

angusticeps), PM (*A. maslini*) and CE (*A. angusticeps*). The T_{sel} means of the *A. rodecki* populations differed significantly from one another and from *A. angusticeps* populations, although the means of both species were higher than those of the other studied species. *Aspidoscelis maslini* populations were characterized by similar T_{sel} means, except for two populations (PM and CK) which were significantly higher. The *A. cozumela* and the *A. deppii* populations were characterized by a similar T_{sel} , which was also similar to most of the *A. maslini* populations.

T_e was significantly different between all study areas ($H = 394.3$, $df = 12$, $p < 0.05$). Populations of *A. angusticeps* inhabit the areas with the highest T_e , without significant differences between them. The *A. rodecki* populations are exposed to low T_e values. T_e significantly differed between *A. maslini* populations. T_e values for *A. cozumela* and *A. deppii* were similar to some *A. maslini* populations (CHA, PM, CK and SK).

We found significant differences in \bar{d}_b across all populations ($H = 74,733$, $df = 12$, $p < 0.05$). The *A. maslini* populations significantly differed from BC and SK. Similar results were observed for *A. rodecki* and for *A. angusticeps* (Table 2).

The environment inhabited by the five studied species significantly differed in \bar{d}_e from each other ($H = 31.138$, $df = 12$, $p < 0.05$). PJ was characterized by the highest \bar{d}_e value, followed by CE and CHE. CZ showed the best thermal quality among all sites, followed by PO, MH and MI. Environments inhabited by *A. maslini* differed significantly from each other. The environments of *A. rodecki* and *A. angusticeps* also showed differences in \bar{d}_e among populations. The environment of *A. deppii* presented less than 3 °C of the \bar{d}_e index.

We identified four groups of populations with similar \bar{d}_e : CZ, PO, MH and MI (≈ 2); CK, BC, PM and IC (≈ 3); SK, CHA, and CHE (≈ 4); CE and PJ (> 5). In the first group, MH had the highest thermal accuracy followed by PO; CZ had the lowest \bar{d}_e index of all populations. In the second group, all populations except BC exhibited low \bar{d}_b indexes; IC had the lowest thermal quality with however the highest precision. The \bar{d}_b of the third group

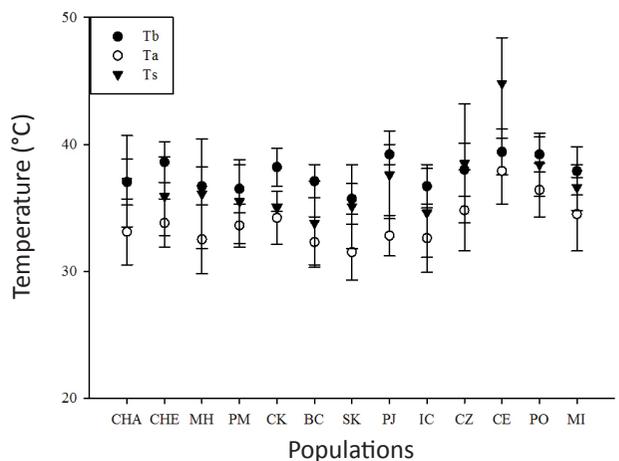


Fig. 5. Mean and standard error of field active body temperature and environmental temperature in the habitat of populations of the *A. cozumela* complex.

increased with $\overline{d_e}$, and in the last group we found the most thermally precise population (PJ) despite having the worst $\overline{d_e}$.

Individuals of the *A. maslini* populations had *E* values ranging from 0.50 in BC to 0.96 in SK; both populations of *A. rodecki* had high *E* indexes (PJ: 0.98 and IC: 0.88). *Aspidoscelis cozumela* had the lowest *E* value in the study. However, both parental species had *E* values below 0.68 (Fig. 6) the lowest values apart from CZ and BC (Table 2).

All populations of *A. rodecki* had high *B-W* values, with indices of thermal stress similar to the three populations of *A. maslini* that inhabit the shore and jungle areas (SK, CHA and CHE). For *A. angusticeps*, CE which inhabits the coastal area had high *B-W*, whereas PO had low *B-W* values. The lowest *B-W* of the study (less than 0.5°C) was observed for *A. cozumela*; *A. deppii* was also characterized by a low *B-W* (Table 2).

DISCUSSION

The parthenogenetic lizards of the *A. cozumela* complex and their parental gonochoristic species are exposed

to high temperatures which provide them the thermal energy for activity (Bowker, 1993). Members of the *A. cozumela* complex and their parental species obtain *T_b* by direct (sun) and indirect basking (substrate contact), and we obtained similar *T_b*s (35.7°C–39.4°C) than a previous study (Woolrich-Piña et al., 2011). Overall high *T_b*s represent their high metabolic requirements (Anderson & Karasov, 1981; 1988; Karasov & Anderson, 1984; Verwajen & Van Damme, 2007; 2008).

Previous studies showed that environmental temperatures are correlated with *T_b* in *Aspidoscelis* (Vitt et al., 1993; Stevens, 1980; 1982; Paulissen, 1999; Güzido-Rodríguez & Casas-Andreu, 2007; Navarro-García et al., 2008; Woolrich-Piña et al., 2011). We showed that most studied species were affected by *T_s*, likely due to heat conduction from the substrate. However, other studies failed to find relationships between *T_b* and environmental temperatures in *Aspidoscelis* (Casas-Andreu & Gurrola-Hidalgo, 1993; Balderas-Valdivia & Ramírez-Bautista, 2002). The influence of *T_a* and *T_s* could vary among populations. Thermoregulatory strategies as well as thermal habitat resources determine *T_b*, which

Table 2. Mean and standard error of field active body temperature (*T_b*), microhabitat air temperature (*T_a*), microhabitat substrate temperature (*T_s*), operative model temperature (*T_e*) and laboratory selected temperature (*T_{sel}*). Interval of the selected temperature between inferior (Inf.) and superior (Sup.) interquartil *T_{set}*. $\overline{d_b}$: Thermal precision; $\overline{d_e}$: quality of the environment; *E*: efficiency Hertz index; *B-W*: Blouin-Demers and Weatherhead effectiveness thermoregulation index; Pop: Population.

Species	Pop	<i>T_b</i>	<i>T_a</i>	<i>T_s</i>	<i>T_e</i>	<i>T_{sel}</i>	<i>T_{set}</i>		$\overline{d_b}$	$\overline{d_e}$	<i>E</i>	<i>B-W</i>
							Inf.	Sup.				
<i>A. maslini</i>	CHA <i>n</i> =38	37.0±1.8	33.1±2.6	37.1±3.6	38.3±6.0	35.3±2.2	34	37	0.77	4.13	0.81	3.36
	CHE <i>n</i> =24	38.6±1.6	33.8±1.9	35.9±3.1	39.6±6.6	35.6±2.6	34.2	37.8	1.23	4.51	0.72	3.27
	MH <i>n</i> =48	36.7±1.5	32.5±2.7	36.1±4.3	35.2±4.8	35.1±2.2	34	36.8	0.60	2.58	0.76	1.98
	PM <i>n</i> =18	36.5±1.9	33.6±1.7	35.5±3.3	38.8±5.4	37.3±1.7	36.4	38.8	0.77	3.47	0.77	2.69
	CK <i>n</i> =19	38.2±1.5	34.2±2.1	35.2±0.3	38.9±5.5	36.4±1.8	35	38	0.69	3.27	0.78	2.58
	BC <i>n</i> =39	37.5±1.3	32.0±2.0	33.6±3.3	36.6±5.3	35.0±1.7	34	36	1.71	3.44	0.50	1.73
	SK <i>n</i> =32	35.7±1.2	31.5±2.2	35.1±3.3	38.4±6.3	34.8±3.0	33	36.8	0.14	4.05	0.96	3.92
<i>A. rodecki</i>	PJ <i>n</i> =20	39.2±0.8	32.8±1.6	37.6±3.5	34.9±6.4	38.8±1.6	38	40	0.08	6.01	0.98	5.93
	IC <i>n</i> =25	36.7±1.7	32.6±2.7	34.6±3.5	35.7±6.1	36.2±2.0	35	37.8	0.45	3.94	0.88	3.49
<i>A. cozumela</i>	CZ <i>n</i> =31	38.0±2.1	34.8±3.2	38.5±4.7	38.0±3.4	35.1±2.3	34	37	1.66	2.02	0.17	0.36
<i>A. angusticeps</i>	CE <i>n</i> =12	39.4±1.8	37.9±2.6	44.8±3.6	39.7±6.0	36.6±1.9	36	38	1.80	5.12	0.64	3.32
	PO <i>n</i> =21	39.2±1.4	36.4±2.1	38.4±2.5	39.9±3.8	37.6±1.7	36.5	39	0.66	2.12	0.68	1.46
<i>A. deppii</i>	MI <i>n</i> =25	37.9±1.9	36.6±2.9	34.5±1.8	38.6±5.0	35.7±2.3	34.1	37.6	0.96	2.93	0.66	1.96

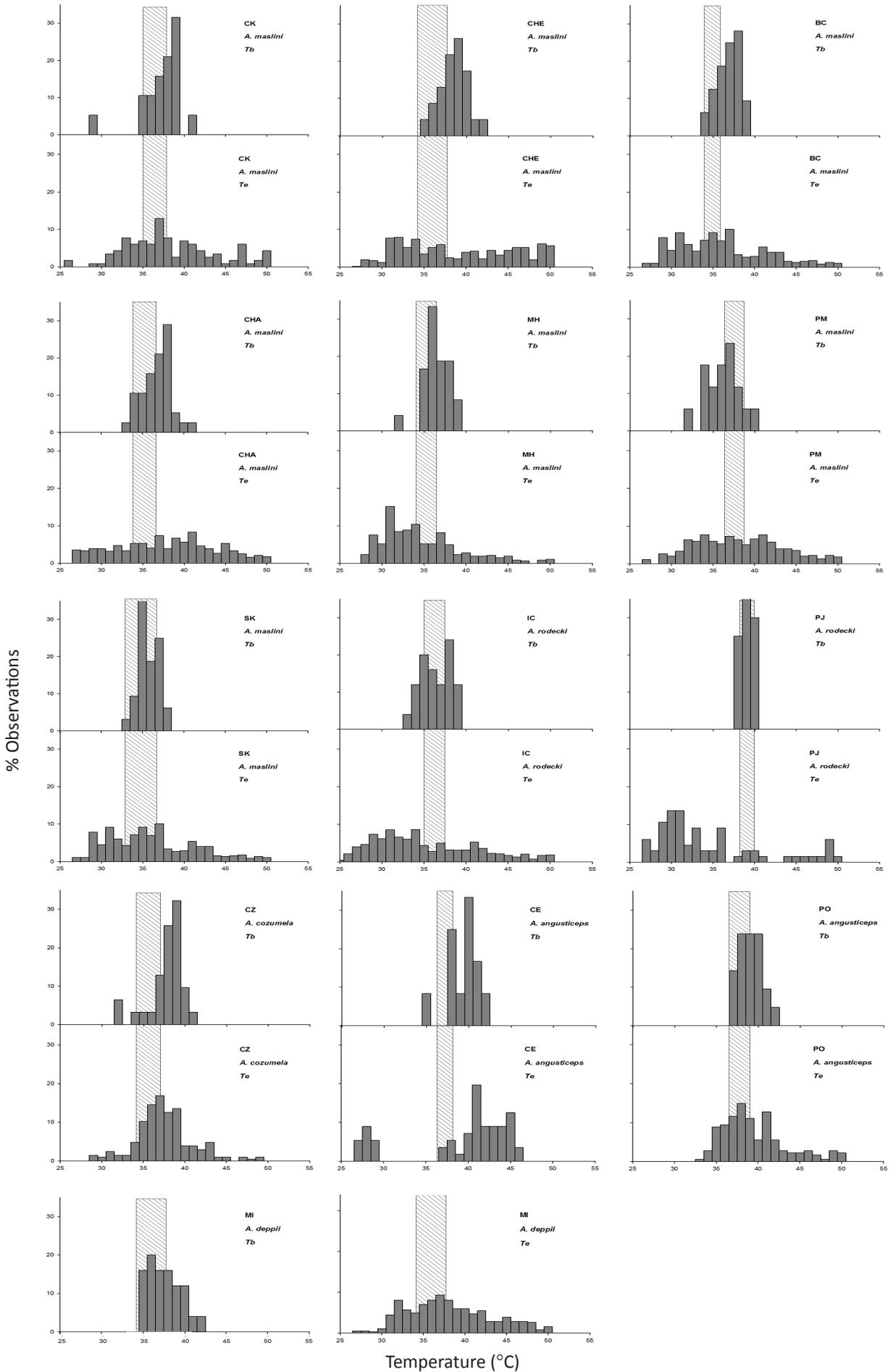


Fig. 6. Distribution of the field T_b and T_e in the microhabitat. The shaded area represents the interval of the selected temperatures T_{set} .

needs to be adequate for physiological processes to ensure population survival.

Lizards should select sites with appropriate thermal quality to avoid high energetic costs (Menezes & Rocha, 2011), and when this is not possible results in thermally stressed populations (Hardie & Hutchings, 2010; Sinervo et al., 2010). Populations of the *A. cozumela* complex and the parental species presented different thermal efficiency indexes, associated with the thermal quality of each area and the lizard's thermoregulatory precision. Some populations of *A. maslini*, *A. rodecki* and *A. angusticeps* are thermally stressed (PJ, CE, CHE, CHA, SK and IC), inhabiting environments with low thermal quality and high *B-W* indices. PJ is the thermally most stressed population of the study ($E=0.98$, $B-W=5.93$), coinciding with the smallest area it inhabits (500 m² surrounded by buildings). However, IC and SK, also inhabiting protected areas, are characterized by low thermal quality.

The rainforest populations of *A. maslini* (CK and CHE) were characterized by the highest *Te* and *Tb* means. *Te* means are similar to *A. angusticeps*, suggesting that *A. maslini* may inhabit areas with similar thermal characteristics. In fact, *A. maslini* and *A. angusticeps* occur in sympatry at CHE. Mean temperatures of *A. angusticeps* from CHE ($n=7$, $Tb=39.2^{\circ}\text{C}$, $Te=38.6^{\circ}\text{C}$, $Tsel=36^{\circ}\text{C}$, $\bar{d}_b=2.66$, $\bar{d}_e=4.2$) were similar to CE and PO, and represented the lowest thermal efficiency index of all parental species ($E=0.36$, $B-W=1.54$), indicating a suitable thermal environment. Individuals of *A. maslini* inhabiting the same area were characterized by a high thermal efficiency index ($E=0.72$, $B-W=3.27$) suggesting they require additional effort to thermoregulate.

Lizards of the *A. cozumela* complex depend on an external source of heat, with thermal preferences being conservative traits among parthenogenetic and parental species. *Aspidoscelis maslini*, *A. cozumela* and *A. deppii* showed similar thermal preferences, whereas *A. rodecki* and *A. angusticeps* had higher requirements, consistent with the FNV hypothesis. Although the same parental species hybridize to form a parthenogenetic species, thermal preferences can be based on the maternal or the paternal species. The similarity of thermal preferences between *A. maslini* and *A. cozumela* coincides with their origin from the same hybridization event (*A. cozumela* is suggested to have its origin from *A. maslini*, Manríquez-Morán, 2002). This coincides with previous studies, which report a close relationship between both species at the molecular level (Moritz et al., 1992; Manríquez-Morán, 2002; Hernández-Gallegos et al., 1998; Manríquez-Morán, 1998). These results also agree with previous work on *Aspidoscelis* and *Cnemidophorus* which described thermal conservatism between related species despite inhabiting different geographical areas (Milstead, 1957; Hardy, 1962; Medica, 1967; Pianka, 1970; Schall, 1977; Bowker & Johnson, 1980; Avery, 1982; Stevens, 1982; Winne & Keck, 2004; Menezes & Rocha, 2011). The lizards counteract the adverse thermal conditions by thermoregulatory behaviour and can occupy habitats that the parental species do not inhabit.

The physiological preferences between parental and parthenogenetic species can be reflected in thermal

efficiency as well as in geographical distributions. The similarity in thermal preference between *A. angusticeps* and *A. rodecki* could limit the distribution of parthenogenetic lineages, as populations are only found in northern areas of the Yucatán peninsula. On the other hand, *A. angusticeps* inhabits a wide area where thermal conditions are more optimal (PO: $\bar{d}_e=2.12$) than in coastal areas (CE: $\bar{d}_e=5.12$). The difference in thermal quality is also reflected in *B-W*. Competition for thermal resources and a younger origin (Manríquez-Morán, 2007; Manríquez-Morán & Méndez-de la Cruz, 2012) could determine the distribution of *A. rodecki*.

The *A. cozumela* complex inhabits zones characterized by the influence of hurricanes (Pielke et al., 2003). Hurricanes rearrange the structure of vegetation, and affect many basic processes influencing animal population size and species composition (Waide, 1991). Parthenogenetic species are considered as good colonizers of unstable environments where parental species are unable to survive (Parker, 1979; Lynch, 1984; Paulissen, 1988; Wright & Vitt, 1993). The three species of the *A. cozumela* complex may be considered as a case where hybrid origin benefits survival under adverse environmental conditions. This capability to inhabit different environments could also be explained by the GPG hypothesis and heterosis. Populations of *A. maslini* (CHE and CK) inhabiting similar thermal quality environments than *A. angusticeps* exhibit similar thermal precision and *B-W* indexes. *Aspidoscelis rodecki* is protected by Mexican law and categorized as Near Threatened by the IUCN, and anthropogenic disturbance currently poses a severe threat to *A. rodecki* populations trapped in thermally adverse environments.

To summarize, the similarities in physiological preferences between *A. cozumela* complex lizards and their parental species support conservatism in thermal preferences in accordance with the FNV hypothesis. The parthenogenetic *A. cozumela* complex successfully inhabits a wide range of environmental conditions, occupying areas where the parental species are absent. Hybrid vigour in combination with thermoregulation seems to facilitate survival in otherwise suboptimal environmental conditions.

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APPENDIX

Appendix 1.

We calibrated the models in laboratory and field conditions. We placed three live lizards and three copper models in a controlled temperature room for three days, taking temperatures every 30 minutes between the active period in the wild (1000–1400 hours). We suspended three 100 W bulbs 50 cm above the substrate to provide a heat source. A fan with constant flow provided cold air (20°C). The voltage of the bulb was varied during the day to produce different heat loads simulating ambient conditions (Hertz, 1992). We found no significant difference between the copper models and live lizards ($t=-0.52$; $df=25$; $p>0.05$). Eighty-five percent of the comparisons between copper model temperatures and lizard T_b differed by less than 1°C. The regression between the T_b of lizards and copper model temperatures was significant ($r^2=85.2$; $n=26$; $p<0.05$). In a second validation experiment, we placed three copper models in the field (BC) with three live lizards at three different environment conditions (sun, middle light and shade). T_b and internal copper model temperature were recorded every 30 minutes during one day (1000–1500 hours). We found no significant difference between T_b and copper model temperatures ($t=1.63$; $df=19$;

$p > 0.05$), but the regression was significant ($r^2 = 90.83$; $n = 20$; $p < 0.05$). Based on the laboratory and field tests, we concluded that the models are a sufficient mimic of the thermal responses of restrained lizards under simulated and field conditions (Dzialowski, 2005).

Appendix 2.

Lizards were exposed to a thermal gradient (25°C to 50°C), within a polycarbonate box (1 m wide x 1.5 m long x 40 cm high). We placed six 150W light bulbs at 50 cm height above one of the gradient ends and two 150 W light bulbs in the middle of the gradient at a height of 70 cm. The other end was left without a heat source in order to generate the thermal gradient. We placed beach sand in the thermal gradient as a substrate, in addition to palm leaves as a shelter, mealworms to induce forage activity of the lizards (we fed the lizards before the test) and small containers with water. This experimental setup simulated the lizards' natural environment, decreasing the stress provoked by the enclosure and allowing them to thermoregulate. Lizards were given one hour to become acclimatized and were captured hourly to measure T_{sel} . This experiment was carried out during the activity period observed in the field (1000 to 1700 hours). We completed all laboratory tests within one or two days after capture (Hertz et al., 1993; Mathies & Andrews, 1995; Stapley, 2006). We obtained the selected temperature intervals (T_{set}) by calculating the interquartile range of all the data of each population.

Appendix 3.

If T_b or $T_e < T_{sel}$, then $db = T_b - T_{sel}_{(low\ limit)}$ and $de = T_e - T_{sel}_{(low\ limit)}$. However, if T_b or $T_e > T_{sel}$, then $db = T_b - T_{sel}_{(high\ limit)}$ and $de = T_e - T_{sel}_{(high\ limit)}$, respectively. When T_b or T_e values were in the 50% of the T_{sel} central interval, then db and de equalled zero. We calculated the mean of all the differences in order to obtain \bar{d}_b and \bar{d}_e . Values of \bar{d}_b and \bar{d}_e equal or close to zero indicate that environments are thermally ideal, while values higher than zero indicating low thermal accuracy and quality. We therefore calculated thermoregulatory efficiency (E) using the equation $E = 1 - (\bar{d}_b / \bar{d}_e)$. The thermal efficiency index ranges from one to zero. A value close to unity means the individuals within the population are active thermoregulators. Therefore, available environmental temperatures do not meet their thermal preferences, resulting in thermal stress. An E index equal or close to zero indicates that the organisms do not require an extra effort to reach their ideal temperature, because thermal quality of the habitat is favourable and satisfies the thermal preference of the lizard (Hertz et al., 1993).

The Blouin-Demers and Weatherhead (2001) index ($B-W$) is defined as the difference between \bar{d}_b and \bar{d}_e to quantify the degree of departure from perfect thermo-conformity. A negative value represents the avoidance of thermally favourable habitats, zero represents perfect thermo-conformity, and a positive value represents animals which thermoregulate.