Thermal ecophysiology of a native and an invasive gecko species in a tropical dry forest of Mexico

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ABSTRACT

For ectotherms, thermal physiology plays a fundamental role in the establishment and success of invasive species in novel areas and, ultimately, in their ecological interactions with native species. Invasive species are assumed to have a greater ability to exploit the thermal environment, higher acclimation capacities, a wider thermal tolerance range, and better relative performance under a range of thermal conditions. Here we compare the thermal ecophysiology of two species that occur in sympatry in a tropical dry forest of the Pacific coast of Mexico, the microendemic species Benedetti's Leaf-toed Gecko (*Phyllodactylus benedettii*) and the invasive Common House Gecko (*Hemidactylus frenatus*). We characterized their patterns of thermoregulation, thermoregulatory efficiency, thermal tolerances, and thermal sensitivity of locomotor performance. In addition, we included morphological variables and an index of body condition to evaluate their effects on the thermal sensitivity of locomotor performance in these species. Although the two species had similar selected temperatures and thermal tolerances, they contrasted in their thermoregulatory strategies and thermal sensitivity of locomotor performance. *Hemidactylus frenatus* had a higher performance than the native species, *P. benedettii*, which would represent an ecological advantage for the former species. Nevertheless, we suggest that given the spatial and temporal limitations in habitat use of the two species, the probability of agonistic interactions between them is reduced. We recommend exploring additional biotic attributes, such as competition, behavior and niche overlap in order assess the role of alternative factors favoring the success of invasive species.

1. Introduction

Although dispersal capabilities, life-history traits, and competitive abilities are some of the main attributes related to the success of invasive species in relation to native species (Rejmánek, 1995; Callaway and Ridenour, 2004), thermal physiology may also play a fundamental role in the establishment of invasive species in novel areas and in their interaction with native species (Kelley, 2014). The thermal environment is particularly important for ectothermic animals, as they rely on environmental temperature to behaviorally thermoregulate and thus sustain basic biological functions, such as metabolism, growth, and locomotion (Huey, 1982). Differences in thermoregulatory characteristics are likely to explain the mechanisms responsible for the invasive potential that introduced ectotherms have over native ones. Such differences include

an enhanced ability to exploit the thermal environment, both spatially and temporally, higher acclimation capacities, wider thermal tolerances (i.e., eurythermality), and enhanced relative performance under a similar range of thermal conditions (Kelley, 2014; Boher et al., 2018).

Specifically, locomotor performance is an ecologically relevant trait, because of the implications it has on evasion of predators, foraging strategies, mate acquisition, exploitation of refuges and habitat exploration (Vanhooydonck and Van Damme, 2003; Miles et al., 2007). In ectotherms, locomotor performance is intimately related to body temperature, as it tends to be optimal in a relatively narrow interval of temperatures and lower at the minimum and maximum thermal tolerance limits (Kaufmann and Bennett, 1989; Ibargüengoytía et al., 2007). As with other physiological parameters, invasive species often outperform native species in terms of their thermal sensitivity to locomotor capacities, which can evolve rapidly to adjust to new local environmental conditions (Kosmala et al., 2017, 2018; Litmer and Murray, 2019). Given the relevance of locomotion on the success of invasive species and their interspecific interactions with native species (Seebacher and Franklin, 2011), locomotor performance represents a useful physiological indicator of the competitiveness of invasive species outside their native range. There are, however, few studies that compare the relative thermal performance of introduced versus native species (Cortes et al., 2016; Boher et al., 2018).

In this study, we examine the differences in the thermal physiology of a microendemic species, the Benedetti's Leaf-toed Gecko (*Phyllodactylus benedettii*), and a widely distributed invasive species, the Common House Gecko (*Hemidactylus frenatus*), which occur in sympatry in a tropical dry forest of Mexico. We hypothesized that the native species would have lower and more specific thermal parameters, a narrower thermal tolerance range, and higher thermal sensitivity of locomotor performance than the invasive species. Based on our results, we discuss the role of thermal physiology in the possible ecological interactions between these lizard species.

2. Materials and methods

2.1. Study species and site

Phyllodactylus benedettii (Ramírez-Reyes and Flores-Villela, 2018; Squamata: Phyllodactylidae) is endemic to the Chamela-Cuixmala Biosphere Reserve, in the state of Jalisco, Mexico. It is a nocturnal species often found in rocks and crevices within the tropical dry forest, but can also occupy human settlements near undisturbed areas. The native distribution of *Hemidactylus frenatus* Duméril and Bibron (1836) (Squamata: Gekkonidae) is southern and southeastern Asia and the Indo-Australian Archipelago. However, it now has a distribution, spanning tropical and subtropical regions (IUCN, 2018). In Mexico, the presence of this species dates back to around 1895, when the first specimen was collected in Acapulco, Guerrero, whereas records from the central Pacific coast are known since the 1960s (Farr, 2011). In contrast to *P. benedettii*, *H. frenatus* is primarily associated with anthropized habitats such as houses and buildings (Case et al., 1994; but see Barnett et al., 2017), mainly because structural complexity of natural habitats reduces its locomotor performance (Petren and Case, 1998; Cole et al., 2005). Bustard (1970) mentions that this species has broad activity periods, which are not restricted by daily temperature fluctuations.

The study site was the Estación de Biología Chamela (EBCh), a scientific station administered by the Universidad Nacional Autónoma de Mexico (UNAM), and located in the Chamela-Cuixmala Biosphere Reserve, on the Pacific coast of the Mexican state of Jalisco (19°29′53″ N, 105°02′40″ O; 90 m elev.). The region is dominated by tropical dry forest (Miranda and Hernández, 1963; Durán et al., 2002), and according with the Köppen climate classification modified by García (1988), the climate is warm sub-humid with summer rains. Mean annual temperature is 24.6 °C, with a minimum average temperature of 19.5 °C and a maximum average temperature of 30 °C. Mean annual

precipitation is 788 mm, with the rainy season occurring from June to October (García-Oliva et al., 2002). As far as we know, EBCh is one of few places in Mexico where a member of the genus *Phyllodactylus* is found in limited syntopy with the invasive *H. frenatus*, which represents an opportunity to address comparative studies between an endemic and an invasive species with similar ecological requirements (Williams et al., 2016).

2.2. Field work

We collected data from 10 to 16 October 2016. We conducted surveys during the observed activity period of the lizards, which in the case of *P. benedettii* was exclusively nocturnal (2000–0500 h) and diurnal/nocturnal in *H. frenatus* (1600–0500 h). We focused our sampling effort on the buildings of the station, where *P. benedettii* and *H. frenatus* co-occur, focusing on wall crevices, window frames, lighting, and air vents, where they were most commonly found. We captured only adult individuals (Ramírez-Bautista et al., 2006; Ramírez-Sandoval et al., 2006), either by noose or by hand. We measured their body (cloacal) temperature (T_b; within 10 s of capture), air temperature (T_a) 3 cm above the substrate, and substrate temperature (T_s), using a digital thermometer Fluke® 54-II with a K thermocouple (±0.1 °C; Fluke Corporation, Everett, Washington, USA) (Woolrich-Piña et al., 2006; Lara-Reséndiz et al., 2013a, b). We recorded time of capture (winter time based) and location, using a GPS device Garmin® eTrex-20 (Garmin, Olathe, Kansas, USA).

We recorded operative environmental temperatures (T_e), the available equilibrium body temperatures of an animal with its environment in the absence of thermoregulation (Dzialowski, 2005), using 11 dataloggers HOBO® U23-003 (HOBO Temp, ONSET Computer Corporation, Bourne, Massachusetts, USA), with previously calibrated biophysical models made of polyvinyl chloride (PVC) pipes filled with industrial silicone (see details in section 2.5 Thermal ecology). We coupled the biophysical models to the sensors of the dataloggers (Dzialowski, 2005; Lara-Reséndiz et al., 2013a; Arenas-Moreno et al., 2018), and placed them in various microhabitats used by both species, with one sensor within and the other one outside the shelter, in order to describe the variation in environmental temperature. We programmed the devices to record T_e every 3 min during a 144 h period.

2.3. Laboratory work

We transported captured individuals to the laboratory of EBCh and housed them in separate terraria (20 × 17 × 12.5 cm) for each species, with leaf litter as substrate and water provided *ad libitu*m. All terraria were kept in a room maintained at approximately 23 °C. We sexed the individuals using a hemipenial transillumination technique (Davis and Leavitt, 2007; Brown, 2009). We measured the following morphological variables of each individual: snout-vent length (SVL), total length (TL), head length (HL), head width (HW), head height (HH), using a digital caliper TITAN® (±0.1 mm; TITAN Professional Tools, Renton, Washington, USA), and mass, with an electronic pocket scale Camry® EHA601 (±0.01 g; Camry Electronic Ltd., Zhaoqing, Guandong, China). We excluded individuals with autotomized tails for the experiments, as tail breaks are known to influence sprint speed (Downes and Shine, 2001).

2.4. Body condition

We estimated the body condition index (BCI) of each species as a measure of the physiological and health status of the organism, for which we followed the scaled mass index method, proposed by Peig and Green (2009, 2010), which standardizes body mass at a fixed value of a linear body measurement based on the scaling relationship between mass and length, applying the following equation:

$$\widehat{M_i} = M_i[L_0 / L_i] \, bSMA$$

where M_i and L_i are the body mass and linear body measurement of individual i, respectively; L_0 is the arithmetic mean of a linear body measurement of the species studied; b_{SMA} is the scaling exponent estimated by standardized major axis (SMA; slope value) regression between M on L; and $\widehat{M_i}$ is the predicted body mass for individual i when the linear body measure is standardized to L_0. We chose L based on the correlation of the morphometrical measurements (SVL, TL, HL, HW, HH) with M, thus we used SVL due to its high correlation (Table A1; Fig. A1-A.3). We used the scaled mass index instead of comparing the residuals from an ordinary least squares (OLS) regression of mass against SVL as is commonly used in body condition studies (e.g., Jakob et al., 1996; Hayes and Shonkwiler, 2001), because this method outperforms the traditional OLS method in estimating BCI (Green, 2001; Peig and Green, 2009).

2.5. Thermal ecology

For the calibration of the biophysical models, we compared the temperature between an immobilized individual lizard and the operative temperature model as they were warmed and cooled. We selected a male lizard from each species and used surgical tape to immobilized it. We also included multiple PVC model candidates (of different size, color, and filled with varying amounts of silicone) in our comparison. We subjected the lizard and each model to 3-min intervals of exposure to artificial light (with a 60 W incandescent light bulb) and then shade during a 3-h period. We used a linear regression to compare the temperature measurements of the models and the lizards (Dzialowski, 2005; Lara-Reséndiz et al., 2013a; Arenas-Moreno et al., 2018). The best resulting model for *P. benedettii* consisted of a white 9.5 cm long × 2.2 cm diameter PVC pipe ($F = 81.83$, df = 28, $b = 0.79$, $R^2 = 0.74$, $P < 0.001$), and a 9.0 cm long × 5.0 cm diameter pipe painted gray 33 for *H. frenatus* ($F = 148.8$, df = 28, $b = 1.69$, $R^2 = 0.84$, $P < 0.001$).

To record the selected temperatures (T_{set}), we used a thermal gradient consisting of a plastic box (90 × 90 × 25 cm) positioned vertically in order to mimic the natural conditions of the habitat, providing cardboard shelters attached to the wall of the enclosure and distributed uniformly across the gradient (Brown, 1996). We carried out the gradient experiments in both light periods of the day-night cycle; during photophase (daytime) we used 250 W incandescent bulb lights and thermal plates, and for the scotophase (nighttime), only thermal plates (Kearney and Predavec, 2000; Lara-Reséndiz et al., 2013a; Arenas-Moreno et al., 2018). The gradient ranged from 23 °C to 40 °C. We recorded T_b of each organism using the same digital thermometer at 2-h

intervals (Brown, 1996), with an acclimation period of 1 h prior to the experiment, during the photophase (1000–1800 h) and scotophase (2100–0500 h) for both species, with a total of 120 measurements by species by phase. We considered T_{set} as the mean body temperature in thermal gradient and also calculated the interquartile range ($T_{set\ 25–75\%}$) as the first and third quartiles of the data. As hydration level during thermal gradient experiments can influence the values of T_{set} of the organisms (Crowley, 1987; Gvoždík and Castilla, 2001), we sprayed the enclosure with water every time we recorded T_{set}.

We used data consisting of T_b, T_{set}, $T_{set\ 25-75\%}$, and T_e to calculate the accuracy of thermoregulation (d_b), the thermal quality of the environment (d_e), and the effectiveness of thermoregulation indexes (Hertz et al., 1993; Blouin-Demers and Weatherhead, 2001). For the calculation of d_b and d_e indices, we contrasted T_b and T_e with T_{set} as follows: if T_b or T_e are lower than the first quartile (25%) of T_{set}, then d_b or d_e equals $T_{set25\%}$ - T_b or $T_{set25\%}$ - T_e, respectively. If T_b or T_e are higher than the third quartile (75%) of T_{set}, then d_b or d_e equals T_b - $T_{set75\%}$ or T_e - $T_{set75\%}$, respectively. When T_b or T_e were within the T_{set} interquartile range, we considered d_b or d_e equal to zero. We then averaged the individual d_b and d_e values to obtain the d_b and d_e indices. High values of d_b or d_e indicate low accuracy of thermoregulation and low environmental quality, respectively, while low values indicate the opposite. From these indices we estimated the Hertz et al. (1993) index using formula $E = 1 - (d_b/d_e)$, as well as the Blouin-Demers and Weatherhead (2001) index, calculated as d_e - d_b. The Hertz et al. (1993) index varies from 0 to 1, where values close to 1 indicate active thermoregulation and those near 0 denote thermoconformity. Positive values of the Blouin-Demers and Weatherhead (2001) index reflect active thermoregulation to some degree and a value of 0 is interpreted as perfect thermoconformity. In both indices, negative values indicate a sub-optimal exploitation of a thermally favorable environment (Hertz et al., 1993; Blouin-Demers and Weatherhead, 2001).

The critical thermal minimum (CT_{min}) and maximum (CT_{max}) refer to the lower and upper temperatures at which there is an impairment in locomotion (Cowles and Bogert, 1944; Kaufmann and Bennett, 1989). We estimated thermal tolerances using only 10 individuals of each species, with a different set of individuals for each tolerance parameter (cold or heat). The lizards used for the thermal tolerance experiments were not previously subjected to gradient experiments. We estimated CT_{min} by placing a lizard inside a perforated plastic box where it could move freely, which in turn was put on top of a container filled with ice. We checked the temperature of the individual every 3 min until there was evident impairment in locomotion, recognizable by a loss of righting response (LRR) within 5 s after laying the lizard on its back (Brown, 1996; Kaufmann and Bennett, 1989; Arenas-Moreno et al., 2018). We used the same criteria for CT_{max}; the individual was placed inside a

Table 1

Thermal parameters of *Phyllodactylus benedettii* and *Hemidactylus frenatus*. Body temperature (T_b); substrate temperature (T_s); air temperature (T_a); selected temperature (T_{set}); interquartile range of T_{set} ($T_{set\ 25-75\%}$); operative temperature (T_e); accuracy of thermoregulation (d_b); thermal quality of the environment (d_e); effectiveness of thermoregulation (*sensu* Hertz et al., 1993; E); effectiveness of thermoregulation (*sensu* Blouin-Demers and Weatherhead, 2001; d_e-d_b). Temperatures (°C) are presented as mean ± SE (minimum value–maximum value; n). Values of T_b, T_a, and T_s for *P. benedettii* (nocturnal species) correspond to the scotophase, whereas the same values for *H. frenatus* (cathemeral species) correspond to both photophase and scotophase.

Species	Period	Field-derived thermal parameters				Laboratory-derived thermal parameters					
		T_b	T_a	T_s	T_e	T_{set}	$T_{set\ 25-75\%}$	d_b	d_e	E	d_e-d_b
P. benedettii	Photophase	29.35 ± 0.15 26.80–31; n = 32	27.09 ± 0.17 24.90–29.0 n = 32	27.37 ± 0.15 25.10–28.90 n = 32	29.55 ± 0.04 23.97–40.25 n = 3360	27.33 ± 0.15 22.40–31.80 n = 30	26.20–28.50	0.95	1.70	0.44	0.75
	Scotophase				28.30 ± 0.03 22.01–36.09 n = 3360	27.04 ± 0.13 23.3–32.8 n = 30	26.05–27.75	1.63	1.04	−0.56	−0.59
H. frenatus	Photophase	30.17 ± 0.20 27.50–32.60 n = 33	27.21 ± 0.22 23.90–29 n = 33	27.50 ± 0.20 24.80–29.40 n = 33	29.39 ± 0.06 23.40–38.95 n = 2400	27.02 ± 0.15 23.60–35.80; n = 30	25.66–27.30	2.78	2.65	−0.04	−0.13
	Scotophase				27.39 ± 0.03 23.76–33.0 n = 2400	27.78 ± 0.20 24.50–35.50 n = 30	26.05–28.60	1.56	0.56	−0.78	−1.00
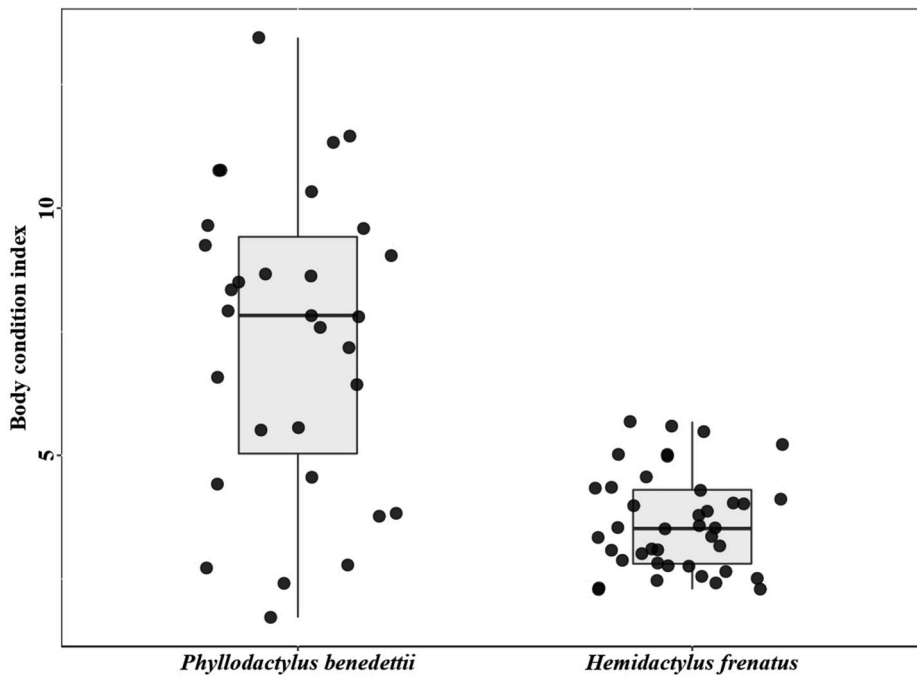
Fig. 1. Body condition index (BCI) of *Phyllodactyulus benedettii* and *Hemidactylus frenatus*. The plot depicts the interquartile range, median, and standard deviation. Black dots are the individual values of BCI.

plastic container, over which a 100 W light bulb was set. Then the lizard was heated up until the LRR, and the body temperature was recorded (Brown, 1996). After the experiments of CT_{min} and CT_{max}, individuals were gradually warmed or cooled (respectively) to bring them closer to the T_{set}. We additionally recorded the panting threshold (PT), which corresponds to the temperature below CT_{max} at which lizards open the mouth widely as a response to heat stress (Heatwole et al., 1973; Brown, 1996). We calculated the thermal tolerance range as the difference between CT_{min} and CT_{max} (Huey and Stevenson, 1979).

2.6. Locomotor performance

We determined the thermal dependence on locomotor performance, measured as sprint speed (m/s), using a vertical trackway (Higham et al., 2011) 120 × 20 × 20 cm made of PVC sheets covered in the bottom with jute (textile fiber) cloth to allow lizards traction during running. Vertical trackways were labelled every centimeter to identify the path run by the lizard. This was done by using a T5 Canon® camera (Canon Inc., Ōita, Ōita, Japan) set to burst mode (Higham et al., 2011) and taking a photograph at every 0.33 s. One person induced lizards to run along the track, by gently touching their pelvic girdle, so that it would not interfere with running speed, while a second person took the photographs. Afterwards, we calculated sprint speed by comparing the distance the lizards ran between successive photographs. We used the distance traveled as the point to the nearest label reached by the snout of the lizard. For each trial, we used 10 adult individuals of each species (we did not use gravid females), which we subjected to three temperature treatments selecting random values, taking into account the thermal tolerance ranges of both species. The first test temperature (V_{T1}) was between CT_{min} and T_{set}; the second temperature (V_{T2}) was within T_{set}, i. e., the interquartile range) and the third temperature (V_{T3}) was between T_{set} and CT_{max}. We set locomotor performance at CT_{min} and CT_{max} as equal to zero. All individuals went through all thermal treatments (Kaufmann and Bennett, 1989; Ibargüengoytía et al., 2007). We processed animals following the guidelines for use of live amphibians and reptiles in field and laboratory research (Beaupre et al., 2004), and at the end of the experiments we released them in their respective site of capture.

2.7. Data analysis

Prior to any statistical analysis, we tested each variable for normality and homoscedasticity of variances through Kolmogorov-Smirnov and Levene's tests, respectively. In the instances where the assumption of normality was not met using transformations, we implemented the appropriate non-parametric tests (Zar, 2010). First, we implemented Mann-Whitney U tests to compare SVL and body mass between species. For the calculation of the body condition index of each species, we estimated the scaling exponent (b_{SMA}) obtained by the regression between body mass (M) and a linear body measurement (SVL; L), using the package 'lmodel2' version 1.7–2 (Legendre, 2014) in R version 3.4.0 (R Development Core Team, Vienna, Austria). We evaluated the differences in BCI between species through a Student's t-test in R.

We compared T_b between sexes using a Student's t-test, and between species, with a Mann-Whitney U test. We performed correlations between T_b and each of the two microhabitat temperatures (T_a, T_s) to determine the main source of heat transfer (convective or conductive) of the two species (Huey and Slatkin, 1976). In order to compare T_{set}, we performed a repeated-measures linear mixed-effects model in SPSS 15.0.1 (SPSS Inc., Chicago, Illinois, USA) with log-transformed T_{set} as response variable, species, sex, and phase (photophase or scotophase) as fixed factors, and measurement in thermal gradient as the repeated measure, as well as their interactions (Kristensen and Hansen, 2004). We compared d_b and d_e between phases for each species through Mann-Whitney U tests (Lara-Reséndiz et al., 2013a). Given the reduced sample size for thermal tolerances, we compared these parameters by species, but not by sex, with Mann-Whitney U tests.

We estimated the thermal sensitivity of locomotor performance by species using general additive mixed models (GAMMs) with the package 'mgvc' version 1.5–6, available within R (Zajitschek et al., 2012). GAMMs fit the relationships between a response variable and a set of predictive variables when there is a non-linear relationship between them, so they are useful to analyze thermal performance curves (Beal et al., 2014; Gilbert and Miles, 2016). We built the models using a Gaussian error distribution with an identity function that includes an autoregressive correlation structure, which serves as an autocorrelation between the sprint speed measures of each individual at the different

temperature treatments (Zajitschek et al., 2012). From the resulting models, we calculated the optimal performance temperatures (T_{opt}), defined as the body temperatures at which performance is maximized, and the thermal performance breadth 80 (B_{80}), the body temperature range in which lizards reach or exceed 80% of sprint speed at T_{opt} (Huey and Stevenson, 1979; Zajitschek et al., 2012).

We evaluated the influence of morphological variables and body condition (explanatory variables) on sprint speed (response variable) in each species with generalized additive mixed models (GAMMs). Before the generation of the GAMMs, we performed a collinearity analysis with the package 'fmsb' version 0.6.3 (Nakazawa, 2018) to discard redundant variables, using a variance inflation factor (VIF) threshold of four. Then, we generated models that represent different combinations of the explanatory variables, using the package 'leaps' version 3.0 (Lumley, 2017). We evaluated these models through the Bayesian Information Criterion (BIC), selecting the variables with the lowest values. Based on the best explanatory variables and the response variable, we generated the GAMMs in 'mgvc' version 1.8–22 (Wood, 2011), and made the selection of the best models through the weights of the Akaike Information Criterion (AIC) and of the BIC, all calculated with functions implemented in R. Finally, we visualized the best models with the function visgam in 'mgvc' version 1.8–22.

We carried out the statistical analyses using the programs R version 3.4.0 (R Development Core Team, Vienna, Austria), SPSS 15.0.1 (SPSS Inc., Chicago, Illinois, USA), and SigmaPlot 11.0 (Systat Software, San Jose, California, USA). For all the tests, we used a significance level <0.05. Throughout the manuscript, values are presented as mean ± SE (range: minimum value–maximum value; n).

3. Results

We collected 35 *P. benedettii* (22 males and 13 females) and 42 *H. frenatus* (26 males and 16 females) that we found sharing the same microhabitats on buildings at EBCh. It is worth mentioning that the following sample sizes do not match the total number of collected individuals. This is because, for some individuals, we were not able to record some thermal and morphometrical variables. Body size was larger for *P. benedettii* than for *H. frenatus* (*P. benedettii*: mean SVL = 62.97 ± 1.61 mm, 45.07–75.64 mm, n = 32; *H. frenatus*: mean SVL = 53.72 ± 0.69 mm, 47–65.76 mm, n = 40; $U = 296.0$, $P < 0.001$), as well as body mass (*P. benedettii*: mean = 7.47 ± 0.58 g, 1.56–12.98 g, n = 31; *H. frenatus*: mean = 3.64 ± 0.16 g, 2.23–5.78 g, n = 40; $U = 203.0$, $P < 0.001$). The body condition index differed between the two species ($t = -6.61$; df = 35.07, $P < 0.001$), with *P. benedettii* showing a higher BCI (mean = 7.37 ± 0.54, 1.72–13.45, n = 31) than *H. frenatus* (mean = 3.63 ± 0.16, 2.29–5.68, n = 40), but also a greater variance on this value than the invasive species (Fig. 1).

Results of T_b, T_s, T_a, T_{set}, T_e, and thermoregulatory indices for both species are summarized in Table 1, while thermal tolerances (CT_{min}, PT, CT_{max}), thermal tolerance range (TTR; $CT_{max} – CT_{min}$), and sprint speed at three temperatures (V_{T1}, V_{T2}, V_{T3}) are presented in Table 2. Individuals of *P. benedettii* were active only during the scotophase, whereas individuals *H. frenatus* were found active both during the photophase and scotophase. In the case of the second species, there were

no significant differences in T_b between day and night ($t = 0.593$, df = 33, $P = 0.557$). T_b was similar between sexes in both species (*P. benedettii*: $t = -0.15$, df = 30, $P = 0.88$; *H. frenatus*: $t = -0.74$, df = 31, $P = 0.47$); however, *H. frenatus* had a higher T_b than *P. benedettii* ($U = 288$, $P = 0.002$). We didn't find any correlation between T_b and microhabitat temperature in *P. benedettii* (T_b vs. T_a: $r = 0.13$, $t = 0.69$, df = 30, $P = 0.49$, n = 32; T_b vs. T_s: $r = 0.26$, $t = 1.48$, df = 30, $P = 0.15$, n = 32; Table A.2; Fig. A.4), but in *H. frenatus* there was a positive and significant correlation between T_b and the temperature of the microhabitat (T_b vs. T_a: $r = 0.67$, $t = 5.24$, df = 33, $P < 0.001$, n = 35; T_b vs. T_s: $r = 0.75$, $t = 6.49$, df = 33, $P < 0.001$, n = 35; Table A2; Fig. A.5). There were not significant interspecific differences in T_{set} by sex, phase, or their interaction (LMM; Table 3).

Thermal quality of the environment (d_e) is high for both species (Fig. 2, Table 1), particularly during the scotophase (*P. benedettii*: $U = 4,854,206$, $P < 0.01$; *H. frenatus*: $U = 1,295,337$, $P < 0.01$). For *P. benedettii*, T_e are higher than the $T_{set25–75\%}$ range both during the photophase and scotophase (photophase: $T_e < T_{set} = 8.30\%$; $T_e = T_{set} = 27.69\%$, $T_e > T_{set} = 64.01\%$; scotophase: $T_e < T_{set} = 6.81\%$; $T_e = T_{set} = 30.33\%$, $T_e > T_{set} = 62.86\%$). In contrast, for *H. frenatus*, only the photophase T_e are above the $T_{set25–75\%}$ range (photophase: $T_e < T_{set} = 9.76\%$; $T_e = T_{set} = 21.16\%$, $T_e > T_{set} = 69.08\%$; scotophase: $T_e < T_{set} = 24.51\%$; $T_e = T_{set} = 52.54\%$, $T_e > T_{set} = 22.95\%$).

Phyllodactylus benedettii was a more accurate thermoregulator during the photophase ($d_b = 0.95$ vs. 1.63; $t = -3.52$, df = 62, $P < 0.001$), while *H. frenatus* had a higher thermoregulatory accuracy during scotophase ($d_b = 1.56$ vs. 2.78; $U = 269.5$, $P < 0.001$). The values obtained of thermoregulatory efficiency (E and $d_e–d_b$) in *P. benedettii* show this species actively thermoregulates during photophase, but have negative values at scotophase. In contrast, *H. frenatus* had negative values during both phases, indicating a suboptimal exploitation of suitable sites (Table 1). With respect to the thermal tolerance parameters, there were no differences in CT_{min} ($U = 25$, $P = 0.06$), PT ($t = -0.82$, df = 13, $P = 0.43$), or CT_{max} ($U = 27.0$, $P = 0.09$) between the two species.

Regarding the locomotor performance, our collinearity analysis showed that mass (VIF = 2650.3), HW (VIF = 26.37), and body condition (VIF = 16.30) of *P. benedettii* were redundant variables, so they were removed from further analyses, while in the case of *H. frenatus*, HH (VIF = 6.62) and body condition (VIF = 12.05) were redundant variables, so

Table 3

Results of the linear mixed-effects model (LMM) of the selected temperatures (T_{set}) of *Phyllodactylus benedettii* and *Hemidactylus frenatus*.

Source	Numerator df	Denominator df	F value	P value
Intercept	1	470	876502.42	<0.0001
Species	1	470	7.07	0.008
Phase	1	470	7.63	0.006
Sex	1	470	0.60	0.44
Species × Phase	1	470	1.30	0.25
Species × Sex	1	470	0.44	0.51
Phase × Sex	1	470	0.15	0.70
Species × Phase × Sex	1	470	0.04	0.85

Table 2

Thermal tolerances and locomotor performance at different temperature treatments of *Phyllodactylus benedettii* and *Hemidactylus frenatus*. Critical thermal minimum (CT_{min}); critical thermal maximum (CT_{max}); panting threshold (PT), thermal tolerance range (TTR; $CT_{max}–CT_{min}$); speed at first temperature treatment (V_{T1} = 20 °C); speed at T_{set} (V_{T2} = 27 °C); speed at third temperature treatment (V_{T3} = 34 °C). Values are presented as mean ± SE (minimum value – maximum value; n). Temperatures are expressed in °C and sprint speeds as m/s.

Species	CT_{min}	PT	CT_{max}	TTR	V_{T1}	V_{T2}	V_{T3}
P. benedettii	15.05 ± 0.75 13–20.50 n = 10	38.30 ± 0.60 36.20–39.50 n = 5	38.94 ± 0.55 35.20–40.80 n = 10	22.99	0.54 ± 0.03 0.27–0.69 n = 10	0.65 ± 0.03 0.48–0.84 n = 10	0.26 ± 0.04 0.09–0.51 n = 10
H. frenatus	16.14 ± 0.31 15–17.9 n = 10	37.68 ± 0.44 35.70–39.50 n = 10	39.99 ± 0.50 36.40–41.50 n = 10	23.85	0.50 ± 0.09 0.12–1.09 n = 10	0.64 ± 0.05 0.39–1.06 n = 10	0.52 ± 0.04 0.24–0.72 n = 10
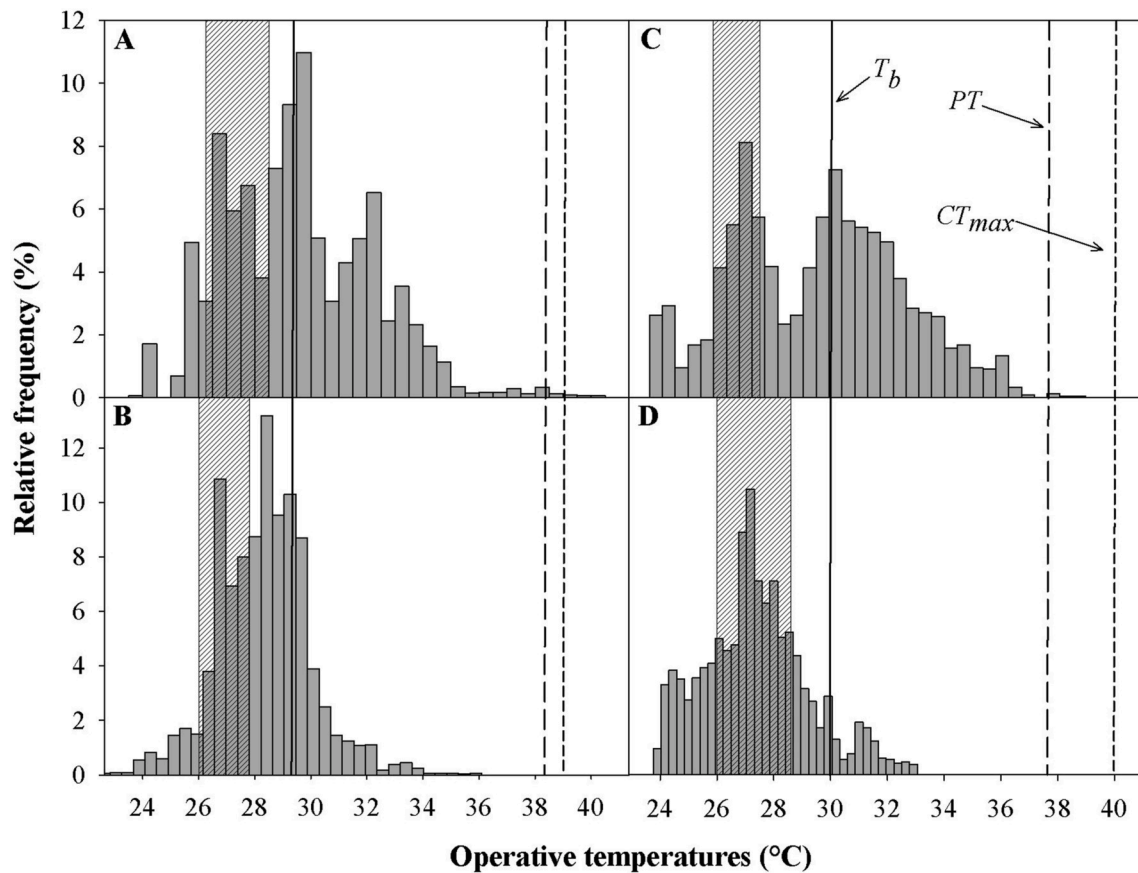
Fig. 2. Operative environmental temperatures (T_e) of the species studied at the Estación de Biología Chamela during the photophase (daytime) and scotophase (nighttime). *Phyllodactylus benedettii* (A = photophase, B = scotophase). *Hemidactylus frenatus* (C = photophase, D = scotophase). The shaded bar represents the selected temperatures ($T_{set25-75\%}$) interquartile range; solid line – mean field body temperature (T_b); long-dashed line – panting threshold (PT), and short-dashed line – critical thermal maximum (CT_{max}).

we discarded these variables from the following analyses. Based on the explanatory variables with the greatest influence on sprint speed (Fig. A.6), we tested 10 different models in each species. In *P. benedettii* the model that included the interaction of TL with temperatures was the model that best predicted the sprint speed in this species (AIC = −89.49, AICc = −87.52, BIC = −78.16, W_{AIC} = 0.28, W_{BIC} = 0.49; Table A3). This model indicated that greater TL is associated with higher values for sprint speed in *P. benedettii*, which only improves in temperature V_{T2} (27 °C), since in V_{T1} and V_{T3} (20 and 34 °C, respectively), the sprint speed decreased drastically (Fig. 3A). On the other hand, in *H. frenatus* the model including the interactions of TL with temperature, as well as the HW and mass, best explained variation in sprint speed (AIC = −43.3, AICc = −39.64, BIC = −27.67, W_{AIC} = 0.57, W_{BIC} = 0.68; Table A.4). The trend showed that for this species, sprint speed increases with TL, but does not exhibit a drastic decrease with temperature (Fig. 3D). Also, HW was positively associated with a higher sprint speed; nevertheless, there is a reduction in sprint speed as mass increases. Although BCI was a redundant variable, given its biological importance we performed a model for each species considering its effect on the thermal performance. The resulting models showed a pattern similar to that obtained for TL, influencing the thermal performance of *P. benedettii* (F = 96.41, df = 49, P < 0.001; Fig. 3B) more than that of *H. frenatus* (F = 52.93, df = 49, P < 0.001; Fig. 3D).

Although both species had similar values for T_{opt}, *P. benedettii* had a narrower performance breadth than *H. frenatus*. *Phyllodactylus benedettii* had a T_{opt} of 24.63 °C, with a maximum predicted speed of 0.76 m/s and a B_{80} of 7.67 °C (range: 20.79–28.46 °C), whereas *H. frenatus* had a T_{opt} of 25.83 °C, with a maximum predicted speed of 0.67 m/s and a B_{80} of 12.45 °C (range: 20.8–33.25 °C).

4. Discussion

The two species showed contrasting thermoregulatory strategies. In *P. benedettii*, body temperature was uncorrelated with micro-enviromental temperatures, a trait consistent with behavioral thermo-regulation, similar to the Yellow-bellied Leaf-toed Gecko (*P. tuberculosus*; Lara-Reséndiz et al., 2013b). In contrast, the significant correlation between body and microenvironmental temperatures in *H. frenatus* indicates that this species does not invest a great effort in achieving and maintaining a temperature different from the environment.

At our study site both species were found in syntopy and with access to wide thermal opportunities during photophase and scotophase. However, unlike *H. frenatus*, which has a cathemeral activity pattern (i. e., both diurnal and nocturnal), *P. benedettii* is only active during sco-tophase, when the thermal quality of the environment is higher. For that reason, this species does not require active thermoregulation during this period, instead spending its energy and time in foraging activities. This is likely the cause of its low exploitation of the thermal environment at night, whereas during the daytime this species seems to select thermal refugia to thermoregulate. This phenomenon has been previously documented in another member of the genus, the Guerreran Leaf-toed Gecko (*P. bordai*), which takes advantage of nighttime temperatures to carry out its activities (e.g., feeding), choosing thermally favorable ref-uges during the day to carry out passive biological processes, such as digestion (Lara-Reséndiz et al., 2013a). The negative thermoregulatory efficiency values of *H. frenatus*, on the other hand, could reflect a lower thermal dependency to perform its basic biological functions, or avoidance of thermally favorable sites because of predators or
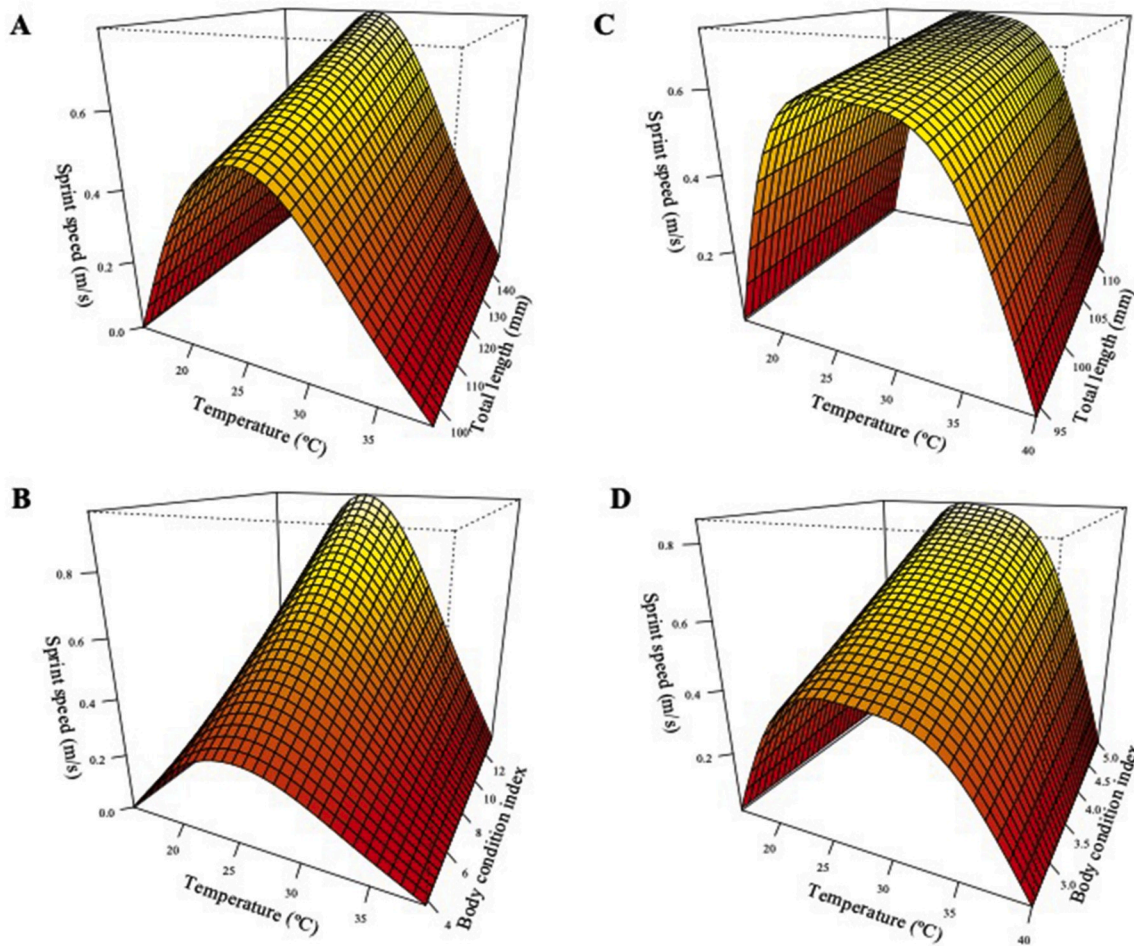
Fig. 3. Thermal performance curves with the effect of total length (mm) and body condition index on the sprint speed (m/s) of *Phyllodactylus benedettii* (A–B) and *Hemidactylus frenatus* (C–D), generated by generalized additive mixed models (GAMMs).

competitors. In the Mediterranean House Gecko (*H. turcicus*), another species introduced to numerous areas outside its native range, some studies have found that intraspecific competition could cause smaller organisms to avoid aggression with larger ones by choosing microhabitats with less favorable temperatures (Regal, 1971; Hitchcock and McBrayer, 2006); however, we don't think this is the case for *H. frenatus* in Chamela, since we observed individuals of different sizes sharing the same microhabitats.

Our results provide partial support for the initial hypotheses that the invasive species exhibits lower physiological specialization than in the native one (Kelley, 2014). For example, although *H. frenatus* had a slightly higher T_b, there were no statistical differences in T_{set} nor in the thermal tolerances of both species, thus rejecting the eurythermality hypothesis. It is possible that the introduced species had adjusted its thermal traits, either by plasticity or adaptation, to match the environmental conditions of the study site, which likely facilitated its establishment and success in this area (Kolbe et al., 2010, 2014). Whether these similarities occur due to the fact that both species share the same habits and exploit the habitat in a similar way, this could only be asserted relying on data from other populations of *H. frenatus* where it is in sympatry with members of the genus *Phyllodactylus*, preferably along environmental gradients (Brown, 1996; Muñoz et al., 2014).

The most conspicuous differences found between the two species were in their thermal dependency on locomotor performance. Sprint speed in *P. benedettii* was more sensitive to temperature than *H. frenatus*, since its sprint speed exhibited a rapid decrease as its body temperature approached the thermal limits and as total body length decreased.

However, *H. frenatus* had its sprint speed less affected by temperature, although smaller individuals showed a higher thermal sensitivity to locomotor performance. Although the optimal temperature for performance did not differ between the species, the thermal breadth (B_{80}) for the invasive species (12.45 °C) was greater than the native species (7.67 °C). Thus, *H. frenatus* could maintain performance at a higher level at a broader range of temperatures than the native species. The observed effect of size on locomotor performance in the two species is similar to a previous study that found an increase in sprint speed with SVL in a Patagonian Gecko (*Homonota darwini*) (Ibargüengoytía et al., 2007).

Few studies have investigated the effect of energetic or nutritional state on the thermal sensitivity of locomotor performance in ectotherms (Gilbert and Miles, 2016). Here we used body condition index as a proxy of the health and nutritional status of the individuals (Peig and Green, 2009, 2010). This variable had a marked differential effect on the shape of the thermal performance curves of the two species, as in *P. benedettii* a lower BCI was associated with a sharp decrease in performance as temperature approaches the critical thermal limits, whereas in *H. frenatus* BCI has little effect on the thermal sensitivity of locomotor performance. The higher variance in the BCI of *P. benedettii* compared to that of *H. frenatus* could indicate better foraging abilities or increased assimilation of nutrients by the second species, despite the sit-and-wait foraging strategy by both species. This assumption is supported by the longer activity period of *H. frenatus* and our own observations of individuals of this species feeding during the daytime, when *P. benedettii* is not active. Also, the ability of *H. frenatus* to perform at higher temperatures likely confers a higher capacity to forage during this period,

further enhancing the physiological performance of this species. Most studies comparing the physiology of native versus introduced ectotherms often rely on the thermal tolerances to infer their intrinsic competitive potential (Kelley, 2014). Given that locomotor performance, and particularly, the thermal performance breadth, was the only thermal parameter that differed between *P. benedettii* and *H. frenatus*, we suggest incorporating this measure in future studies dealing with the comparison of native and invasive species.

In the present work we did not considered acclimatization effects on the traits included in our analysis, which in a seasonal environment, such as that of the tropical dry forest of Chamela, might influence the physiological responses of ectotherms (Arenas Moreno, 2014). We hence suggest incorporating this approach to future studies dealing with the thermal ecology of these lizards. In summary, these results show, from an integrated ecophysiological view, that *H. frenatus* is less sensitive to temperature fluctuations in performing some of its basic biological functions (feeding and locomotion) than the native species, *P. benedettii*. These traits could reflect the success this species has had in colonizing novel environments outside its original distribution range, and also the advantage it might have over native species under scenarios of climate change (Gilbert and Miles, 2016; Kelley, 2014). It must be emphasized, however, that the ability of *H. frenatus* of being diurnally active likely minimizes the occurrence of agonistic interactions between both species; the same happens from the opposite end, because in contrast to *H. frenatus*, which at the study site is exclusively associated to anthropized habitats, *P. benedettii* can exploit resources in the forest interior in the absence of temporal or spatial overlap. More studies are needed in order to confirm or discard the existence of competitive interactions between these geckos, and it would be interesting to make a comparison of the thermal ecology of *P. benedettii* from the Chamela station and from the forest, which was beyond the scope of this study. We recommend further investigation in activity patterns, feeding behavior and niche overlap in order to determine the role of other factors, such as interspecific competition, that may affect the invasion success of *H. frenatus*.

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Declaration of competing interest

The authors declare no conflicts of interest.

CRediT authorship contribution statement

Óscar Romero-Báez: Conceptualization, Investigation, Funding acquisition, Methodology, Software, Data curation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Rufino Santos-Bibiano:** Conceptualization, Investigation, Funding acquisition, Methodology, Software, Data curation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Miguel Adrián Domínguez-Godoy:** Conceptualization, Investigation, Funding acquisition, Methodology, Data curation, Formal analysis, Visualization, Writing - original draft. **Donald B. Miles:** Funding acquisition, Data curation, Software, Formal analysis, Visualization, Validation, Writing - review & editing. **Francisco Javier Muñoz-Nolasco:** Conceptualization, Investigation, Funding acquisition, Methodology, Software, Data curation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing, Supervision.

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Appendix A. Supplementary data

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