

# Thermoregulation and thermal performance of crested geckos (*Correlophus ciliatus*) suggest an extended optimality hypothesis for the evolution of thermoregulatory set-points

Andrea Aparicio Ramirez | Karina Perez | Rory S. Telemeco 

Department of Biology, California State University Fresno, Fresno, California

## Correspondence

Rory S. Telemeco, Department of Biology, California State University Fresno, Fresno, CA 93740.

Email: [telemeco@csufresno.edu](mailto:telemeco@csufresno.edu)

## Funding information

California State University Fresno

## Abstract

Crested geckos (*Correlophus ciliatus*, formerly *Rhacodactylus ciliatus*) were rediscovered in New Caledonia 25 years ago and despite being common in the pet trade, there is no published information on their physiology. We measured thermoregulation (preferred body temperature, thermal set-point range, and voluntary limits) and performance (thermal performance curves [TPC] for 25 cm sprint speed and 1 m running speed) of adult and juvenile crested geckos in the laboratory to describe their thermal tolerances, differences among life stages, correlations between behavior and performance, and correlations with natural temperatures. Despite lacking special lighting or heating requirements in captivity, crested geckos displayed typical thermal biology for a lizard with no difference among life stages. They thermoregulated to a narrow set-point range ( $T_{\text{SET}}$ , 24–28°C), that broadly overlaps natural air temperatures in New Caledonia, during activity. Somewhat surprisingly, the optimal temperature for performance ( $T_{\text{OPT}}$ , 32°C) was substantially above preferred body temperatures and approximated the average maximum temperature voluntarily experienced ( $VT_{\text{MAX}}$ , 33°C). Preferred body temperatures, by contrast, corresponded to the lower threshold temperature ( $T_d$ ) where the TPC deviated from exponential, which we suggest is the temperature where performance is optimized after accounting for the costs of metabolic demand and overheating risk. Our results demonstrate that despite their lack of specific requirements when housed in human dwellings, crested geckos actively thermoregulate to temperatures that facilitate performance, and have thermal biology typical of other nocturnal or shade-dwelling species. Additionally, crested geckos appear at little risk of direct climate change-induced decline because increased temperatures should allow increased activity.

## KEYWORDS

beta equation, lizard, New Caledonia, running performance, thermal performance curve, voluntary thermal limits ( $VT_{\text{MAX}}$  and  $VT_{\text{MIN}}$ )

## 1 | INTRODUCTION

Because body temperature affects virtually all fitness-linked processes, thermal environment is an important selection pressure that defines a major axis of the fundamental niche (reviewed in Angilletta, 2009; McNab, 2002). Moreover, the thermal environment has proven highly dynamic in the Anthropocene, changing as a result of both direct habitat alteration and ongoing climate change (IPCC, 2013; Lewis & Maslin, 2015; Steffen et al., 2018). Thus, a necessary step for understanding both a species' evolutionary history and prospect for long-term persistence is to quantify the effects of temperature on behavior and performance (Bowler & Terblanche, 2008; Gunderson & Stillman, 2015; Taylor et al., 2020; Urban, Richardson, & Freidenfelds, 2014). This is especially true for endemic, tropical species that are poorly studied, live in at-risk habitat, and could have different thermal biology from widespread temperate species which tend to be better studied (although see substantial research on Caribbean *Anolis* for a tropical exception). Here, we describe the thermal biology of such an endemic, the New Caledonian crested gecko, *Correlophus ciliatus* (formerly *Rhacodactylus ciliatus*).

The effect of body temperature on performance in ectotherms is classically described via the thermal performance curve (TPC; all abbreviations are described in Table 1; Huey & Stevenson, 1979). In reptiles, TPCs are typically left-skewed and unimodal with whole-organism performance slowly increasing with body temperature above the critical minimum ( $CT_{MIN}$ ) until an optimum temperature ( $T_{OPT}$ ) is reached where performance is maximized ( $W_f$ ). Performance then rapidly falls at temperatures above  $T_{OPT}$  until reaching zero at the critical thermal maximum ( $CT_{MAX}$ ). Although the general shape of this relationship is well conserved, specific parameter values can vary widely, both within and among species and even across the life span of individuals (Careau, Biro, Bonneaud, Fokam, & Herrel, 2014; Dowd, King, & Denny, 2015; Klockmann, Günter, & Fischer, 2016; Rezende, Castañeda, & Santos, 2014; Sinclair et al., 2016). Thus, to understand how variation in the thermal environment affects

populations, we must describe the average effects of temperature on performance as well as the variation, particularly among age classes.

The TPC is predicted to evolve such that performance is optimized at temperatures typically experienced by organisms (Angilletta, 2009; Gilchrist, 1995). However, most animals do not directly experience average environmental temperatures, but instead alter their body temperatures via thermoregulation (Angilletta, 2009; Huey & Slatkin, 1976). Reptiles and other ectotherms primarily thermoregulate behaviorally by shuttling between thermal micro-environments (Cowles & Bogert, 1944; Huey & Slatkin, 1976). Because of their close link, the TPC and thermoregulatory behavior are expected to coevolve, with thermoregulation under selection to optimize performance given the TPC, and the TPC under selection to optimize performance given body temperatures experienced via thermoregulation (reviewed in Angilletta, 2009). Selection on thermoregulation is expected to limit exposure to extreme or dangerous temperatures thereby allowing persistence in diverse thermal environments, but this reduces natural selection for increased thermal tolerance (i.e., the Bogert effect; Huey, Hertz, & Sinervo, 2003; Muñoz & Losos, 2018). As a result of this coevolution, individuals are expected to thermoregulate such that body temperatures closely match optimal temperatures during activity, so long as suitable thermal microenvironments are available and costs are minimal (Basson, Levy, Angilletta, & Clusella-Trullas, 2017; Huey & Slatkin, 1976; Sears et al., 2016). Optimal temperatures for thermoregulation could be those that maximize performance or those that maximize net performance after accounting for costs such as overheating risk (Angilletta, 2009; Huey & Bennett, 1987; Martin & Huey, 2008). Regardless, tight thermoregulation shields individuals from natural selection for increased tolerance to extreme temperatures, potentially resulting in narrow thermal tolerance breadth (Buckley & Huey, 2016; Muñoz et al., 2016; but see Logan, Cox, & Calsbeek, 2014).

Many environments, however, either do not allow or do not require such tight thermoregulation, potentially allowing increased selection on thermal tolerance. In the tropics, the temperature tends

Abbreviation	Description
$CT_{MAX}$	Critical thermal maximum. Here, $CT_{MAX}$ was estimated as the temperature where the TPC for running performance is predicted to drop to zero
PBT	Preferred body temperature
$T_d$	Temperature of deviation from exponential. TPCs have both an upper and lower $T_d$
$T_{OPT}$	Optimum temperature where performance is maximized
TPC	Thermal performance curve
$T_{SET}$	Thermal set-point range
$VT_{MAX}$	Voluntary thermal maximum
$VT_{MIN}$	Voluntary thermal minimum
$W_f$	Peak performance. Occurs at the optimum temperature

Note: Additional details are available in the main text.

**TABLE 1** Abbreviations and their descriptions

to be relatively stable and warm throughout the year (Buckley & Huey, 2016; Pincebourde & Suppo, 2016; Sunday, Bates, & Dulvy, 2011). In such situations, animals might not need to actively thermoregulate to maintain suitable body temperatures, and there should be little selection for either tight behavioral thermoregulation or broad thermal tolerance (Buckley & Huey, 2016; Huey & Slatkin, 1976). By contrast, nocturnal species are expected to experience little thermal heterogeneity, but possibly cooler temperatures than diurnal species (Gunderson & Stillman, 2015). Because thermal heterogeneity is required for behavioral thermoregulation, this situation is expected to result in little selection for behavioral thermoregulation, but strong selection for performance at relatively cool temperatures. Additionally, life history stages may vary in their capacity to thermoregulate, thermoregulatory set-points, or the costs associated with thermoregulation. As an extreme example, developing embryos of oviparous species cannot access thermal microenvironments outside of the egg (Cordero, Telemeco, & Gangloff, 2018; Telemeco et al., 2016). Even free-living juveniles might not be able to thermoregulate as freely as adults because of increased predation risk or other constraints. In such situations where the capacity to thermoregulate is reduced but exposure to variable thermal microenvironments is high, we expect selection for increased thermal performance breadth (Buckley & Huey, 2016; Gilchrist, 1995).

Crested geckos are large geckos (~35 g) endemic to tropical forests of southeastern New Caledonia (Bauer & Sadlier, 2000). To date, no published information is available about the physiology, life history, or thermal ecology of crested geckos, and little information is available about their natural history. Although first described in the mid-19th century, crested geckos were presumed extinct for ~150 years before being rediscovered in 1994 (Bauer & Sadlier, 2000; de Vosjoli, 2005). A handful of animals were exported to the United States and Europe between 1994 and 1996, almost entirely from their largest population on the Isle of Pines (Ile des Pins), before exportation was banned (de Vosjoli, 2005). These captive geckos bred readily, and crested geckos are now one of the most popular species in the commercial pet trade (de Vosjoli, 2005; Team, 2017). A major reason for their popularity as pets is that crested geckos thrive in human homes without additional lighting or heating requirements, unlike most reptiles in the pet trade (Team, 2017). This capacity suggests that crested geckos might be broad thermal generalists, possibly because their natural habitat (treetops in the tropics at night) offers minimal thermal heterogeneity. However, pet care manuals also suggest that crested geckos perform best with temperatures between 25°C and 28°C during activity and as low as 15°C during inactivity (de Vosjoli, 2005; de Vosjoli & Repashy, 2014; Team, 2017). Thus, crested geckos could be thermal specialists whose success as pets results from their thermal requirements aligning with temperatures typically maintained within human homes.

We tested the hypothesis that crested geckos are thermal generalists by quantifying thermoregulation and thermal performance in the laboratory for two life-history stages (juvenile and adult) of

captive-reared crested gecko and compared those with air temperatures in New Caledonia. We predicted that crested geckos would not actively thermoregulate and maintain high performance across temperatures commonly experienced. Furthermore, because juveniles can be harassed or even eaten by adults (de Vosjoli, 2005; Team, 2017), potentially forcing them to inhabit marginal habitats, we predicted that juveniles would have broader thermal performance breadth than adults. Finally, we directly compared thermal behavior and performance to illuminate how natural selection has shaped thermal set-points in this species. Based on this comparison, we propose that natural selection shapes thermoregulatory set-points to approximate the lower inflection point on the TPC (lower  $T_d$ ) because performance benefits should most outweigh the costs of metabolic demand and overheating risk at this temperature.

## 2 | METHODS

### 2.1 | Animal acquisition and maintenance

We obtained adult crested geckos from commercial breeders in Fresno, CA in March 2018 and transported them to the laboratory at California State University, Fresno. All animals were ~1 year of age at acquisition and the result of captive breeding, likely for many generations. Before experiments were carried out, adult geckos ( $N = 18$ ; females = 9, males = 9) were housed in captivity for ~11 months and were ~2 years old at the start of the trials. We performed trials with  $N = 17$  juveniles produced from the eggs of these adults, and these juveniles ranged from 7.2 to 9.4 months of age at the start of the trials. One juvenile died before its final trial, and data are only included in the analyses for which it was alive.

Before conducting the experiments, animals were housed in a climate-controlled room with temperature maintained at ~25–27°C, relative humidity of ~60%, and a 12:12 inverted light cycle (lights on from 18:00 to 6:00). Lizards were housed in glass enclosures with wire mesh tops (45.72 × 45.72 × 60.96 cm,  $L \times W \times H$ ) in groups of either one male and two females, or one male and one female. Adult lizards were uniquely marked with visual implant elastomer (VIE) tags (Northwest Marine Technology Inc., Shaw Island, WA) injected under the skin of the limbs for permanent identification. Enclosures were outfitted with artificial greenery and egg carton for climbing and hiding, and a mixture of moist peat moss and vermiculite for oviposition. We obtained eggs from six females and incubated them in vermiculite with a water potential of ~150 kPa (Telemeco, 2014) at room temperature (~20°C). Hatchlings were not marked with VIE but were instead housed individually for identification, initially within 16-oz plastic cups with mesh lids and then in 32-oz plastic cups with mesh lids after 2 months. An egg crate was placed within these cups to provide climbing structures and hides. All enclosures were misted with water twice daily to ensure ad libitum water availability and high humidity within enclosures. We provided all geckos a fresh dish of crested gecko diet (Breeding Formula for Reproductive Adult Geckos; Pangea Reptile LLC; mixed by following manufacturer's

instructions) every other day, and we provided 3–5 live crickets once per week. We measured snout–vent length and mass, and visually checked calcium glands monthly to monitor development and health.

## 2.2 | Thermoregulatory behavior

We quantified thermoregulatory behavior by measuring body temperature at 10-s intervals while lizards thermoregulated within a controlled thermal gradient for 2.5 hr during their diel activity period. All thermoregulation trials took place from November 10 to 21, 2018 with a random mixture of juveniles and adults tested each trial day. Crested geckos do not display a distinct reproductive period in captivity and can reproduce year-round, thus trials were conducted during the reproductive period (de Vosjoli, 2005; Team, 2017). Thermal gradients were maintained within boxes ( $110 \times 60 \times 30.5$  cm,  $L \times W \times H$ ) with opaque plexiglass walls and transparent lid, and an aluminum base set on 2" extruded polystyrene foam. The gradient was longitudinally divided with opaque barriers into four, 15 cm wide lanes, allowing simultaneous measurement of four geckos. We created the temperature gradients by placing 310–330 g dry ice on one side of the aluminum base outside of the gradient (i.e., physically separated from the lizards) and suspending 150W ceramic heat emitters 14 cm above each lane on the opposite side. To prevent extreme temperatures, we placed a sheet of cardboard on the aluminum base nearest the dry ice and connected the heat emitters to a thermostat (DBS-1000; Helix Control Systems). This resulted in each lane maintaining a thermal gradient of 10–41°C. Because crested geckos are nocturnal, all trials took place during the dark period of their diel cycle and the room was darkened during trials. Additionally, the room housing the thermal gradients was maintained at ~21°C. During trials, we attempted to remain silent and out of the geckos' sight, but frequently misted the gradients with water to prevent dehydration.

At the start of each thermoregulation trial, we installed the dry ice, turned on the heat emitters, and introduced the geckos then waited 30 min for gradients to form and lizards to acclimate before recording body temperature data. We measured body temperature by placing thermistor probes (PT907; Pace Scientific) attached to data loggers (XR5-SE-20 mV, system accuracy =  $\pm 0.15^\circ\text{C}$ ; Pace Scientific) preprogrammed to record temperature every 10 s in the groin between the left thigh and cloaca. These thermistor probes were secured in position with medical tape which was removed after trials using 70% ethanol to dissolve the adhesive. In small- to medium-sized lizards, groin temperature is a reliable proxy for cloacal temperature and has reduced risk of discomfort or injury (Camacho et al., 2018). For each individual, we used data from their final 2.5 hr in the gradients to estimate the preferred body temperature (PBT) as the mean temperature experienced, the thermal set-point range ( $T_{\text{SET}}$ ) as the 25–75% interquartile range (Hertz, Huey, & Stevenson, 1993; Ivey et al., 2020), and the voluntary thermal minimum and maximum as the lowest and highest body temperatures experienced, respectively (Camacho et al., 2018).

## 2.3 | Thermal performance

As a proxy of whole-organism performance and neuromuscular function, we quantified the effects of temperature on running speed for each lizard across two distances (20 cm and 1 m) at five temperatures (20°C, 24°C, 28°C, 32°C, and 36°C). Running trials were conducted from January 26, 2019 to February 9, 2019, ~2 months after the thermoregulation trials, and with the same lizards. Temperatures were chosen based on the results from the thermoregulation trials to encompass the full range of body temperatures selected by the lizards. For trials, the lizards were randomly assigned to one of the five blocks, with 6–7 individuals per block and each block was exposed to the five temperatures in a different order. We manipulated body temperature by placing the lizards in precalibrated incubators (four Memmert IPP110 plus and one Percival 136VL), and each incubator maintained the same temperature across trials. Before measuring performance, lizards were placed in their respective incubator for 1.5 hr in small plastic containers ( $10.16 \times 12.7 \times 15.24$  cm,  $L \times W \times H$ ) to equilibrate with the test temperature. Although we did not monitor  $T_b$  of the animals within incubators during performance trials, a pilot study with our largest gecko demonstrated that 1.5 hr was sufficient to reach thermal equilibrium at all test temperatures. Lizards were then run on a custom 1.2 m racetrack (10 cm wide) with six infrared sensors placed every 20 cm (Trackmate Racing) by following standard protocols (e.g., Elphick & Shine, 1998; Telemeco, 2014; Telemeco, Baird, & Shine, 2011). For each temperature, lizards were raced three times, with at least 15-min rest between successive runs. While resting, lizards were returned to their incubator to maintain their test body temperature. To limit temperature reduction from frequently opening incubator doors, we tested one lizard from each treatment before cycling back and testing additional lizards. We waited 4 days between trials at different temperatures to allow lizards time to rest and recover, during which lizards continued to be provided food paste every other day. Similar to the thermoregulation trials, all racing trials were conducted during the lizards' activity period in a darkened room. From these data, we quantified the mean fastest 20 cm speed and mean 1 m speed for each individual at each temperature.

## 2.4 | New Caledonia climate

To characterize the thermal conditions experienced by crested geckos in the wild, we downloaded daily air temperature summaries for Noumea, New Caledonia from January 1989 through June 2009 (most recently available) from the NOAA climate data portal ([ncdc.noaa.gov](https://www.ncdc.noaa.gov)). The weather station at Noumea is the closest available station to Ile des Pin, home to the largest remaining wild population of crested geckos and where most captive stock was presumably sourced (Bauer & Sadler, 2000; de Vosjoli, 2005). Moreover, given their close proximities to the ocean, air temperatures between these two sites should be highly conserved. Although air temperature

typically is a poor proxy for body temperature in lizards (Angilletta, 2009; Taylor et al., 2020), air temperature should be a reasonable proxy in crested geckos because they are arboreal and nocturnal. Arboreality removes any direct impact of ground temperature on body temperature, and both arboreality and nocturnality reduce the impact of radiative heat exchange on body temperature (Angilletta, 2009; Gunderson & Stillman, 2015). We used these data to calculate 20-year summary statistics for daily maximum and minimum air temperature and graphically compared these with laboratory results for thermoregulatory behavior and performance.

## 2.5 | Analyses

We performed all analyses using program R version 3.6.1 (R Core Team, 2019). Data for all analyses are available as online Supporting Information. To test for ontogenetic changes in thermoregulatory behavior, we used Welch's two-sample *t* tests (*t.test* function) to compare the PBT,  $T_{SET}$  range,  $VT_{MIN}$ , and  $VT_{MAX}$  of juvenile and adult geckos. For adult geckos, we similarly used Welch's two-sample *t* tests to compare the effect of sex on each measure of thermoregulatory behavior. We only examined the effect of sex in adults because we were unable to determine the sex of juveniles. For thermal performance, we first fit the beta equation TPC model (Yan & Hunt, 1999) to the mean fastest 20 cm and mean 1 m running speed data for each individual using the *nls* function in R. This allowed us to estimate optimum temperature for performance ( $T_{OPT}$ ), maximum performance ( $W_f$ ), and critical thermal maximum temperature where performance dropped to zero ( $CT_{MAX}$ ) for each gecko and speed estimate. Notably, this  $CT_{MAX}$  estimate represents when running performance is expected to be zero, not necessarily when

the animal is unable to right itself. We modeled the TPC using the beta equation rather than other candidate TPC models because the beta equation best fits performance data in diverse lizard species and produces readily interpretable parameter estimates (Tomlinson, 2019). We were unable to fit the beta equation or nonsensical parameter estimates were returned for a few individuals, and we dropped these individuals from subsequent analyses leaving a total  $N = 14, 12, 10,$  and  $12$  for adult and juvenile mean fastest 20 cm speed, and mean 1 m speed, respectively. We used multivariate analysis of variances (*lm* function) to compare the TPC of adults and juveniles for each speed measure using a matrix of  $T_{OPT}$ ,  $W_f$ , and  $CT_{MAX}$  scaled with a mean of zero and unit variance as the dependent variable (Legendre & Legendre, 2012). Finally, we used Welch's two-sample *t* tests to compare each parameter estimate between adults and juveniles, between adult males and adult females, and between 20 cm and 1 m performance measures.

## 3 | RESULTS

Thermoregulatory behavior did not differ between adult and juvenile crested geckos (Table 2;  $p > .07$  for all comparisons), or between adult males and females (Table 3;  $p > .35$  for all comparisons). Pooled across age and sex, PBT was  $26.09 \pm 3.98^\circ\text{C}$  (grand mean  $\pm$  standard deviation [*SD*]) with  $T_{SET}$  ranging from  $24.19 \pm 4.29^\circ\text{C}$  to  $27.92 \pm 4.24^\circ\text{C}$ .  $VT_{MIN}$  was  $17.72 \pm 5.15^\circ\text{C}$  and  $VT_{MAX}$  was  $33.27 \pm 3.01^\circ\text{C}$  (Figure 1a). TPCs also did not differ between the age classes for either mean fastest 20 cm (Pillai's trace = 0.060;  $df = 1$ ;  $p = .7093$ ) or mean 1 m speed (Pillai's trace = 0.066;  $df = 1$ ;  $p = .7381$ ; Table 3), and none of the TPC parameters differed between adult males and females (Table 3;  $p > .10$  for all comparisons). Comparing speed

**TABLE 2** Results from Welch's two-sample *t* tests comparing measures of thermoregulatory behavior and TPC parameters among adult and juvenile crested geckos, *Correlophus ciliatus*

Measure	Adult	Juvenile	<i>t</i> value	<i>df</i>	<i>p</i> value
PBT	26.73 $\pm$ 2.93	25.4 $\pm$ 4.87	0.917	22.667	.3678
$VT_{MAX}$	32.99 $\pm$ 3.16	33.56 $\pm$ 2.93	-0.522	28.998	.6059
$VT_{MIN}$	19.29 $\pm$ 5.23	16.04 $\pm$ 4.65	1.8333	28.925	.0771
$T_{SET}$ range	3.37 $\pm$ 1.62	4.12 $\pm$ 2.19	-1.0791	25.735	.2906
20 cm $T_{OPT}$	32.29 $\pm$ 2.95	31.58 $\pm$ 5.21	0.42299	16.804	.6777
20 cm $W_f$	0.45 $\pm$ 0.29	0.45 $\pm$ 0.23	0.025844	23.85	.9796
20 cm $CT_{MAX}$	39.41 $\pm$ 3.78	41.42 $\pm$ 5.85	-1.0214	18.308	.3204
1 m $CT_{OPT}$	32.27 $\pm$ 2.54	32.63 $\pm$ 2.95	-0.30765	19.963	.7615
1 m $W_f$	0.28 $\pm$ 0.22	0.24 $\pm$ 0.12	0.44118	13.184	.6662
1 m $CT_{MAX}$	38.67 $\pm$ 2.74	40.13 $\pm$ 3.06	-1.1867	19.867	.2493

Note: TPC were estimated by fitting the beta equation to running speed across 20 cm (mean fastest) and 1 m (mean) distances at five temperatures. Values in the "Adult" and "Juvenile" columns are mean  $\pm$  *SD*. for each measure ( $^\circ\text{C}$  for all but  $W_f$  which is m/s).

Abbreviations:  $CT_{MAX}$ , critical thermal maximum; PBT, preferred body temperature; *SD*, standard deviation;  $T_{OPT}$ , optimum temperature where performance is maximized;  $T_{SET}$ , thermal set-point range; TPC, thermal performance curve;  $VT_{MAX}$ , voluntary thermal maximum;  $VT_{MIN}$ , voluntary thermal minimum;  $W_f$ , peak performance.

Measure	Male	Female	t value	df	p value
PBT	26.94 ± 3.38	26.99 ± 2.69	-0.027	9.088	.9792
VT <sub>MAX</sub>	32.33 ± 4.00	33.57 ± 2.79	-0.657	8.22	.5290
VT <sub>MIN</sub>	17.50 ± 6.79	20.54 ± 4.28	-0.974	7.661	.3598
T <sub>SET</sub> range	3.48 ± 1.54	3.41 ± 1.81	0.075	12.071	.9413
20 cm T <sub>OPT</sub>	32.59 ± 1.88	32.16 ± 4.28	0.223	6.869	.8301
20 cm W <sub>f</sub>	0.54 ± 0.39	0.40 ± 0.24	0.755	8.2504	.4712
20 cm CT <sub>MAX</sub>	37.93 ± 1.46	41.84 ± 4.70	-1.944	5.952	.1002
1 m T <sub>OPT</sub>	32.79 ± 2.15	31.73 ± 3.30	0.499	3.054	.6515
1 m W <sub>f</sub>	0.25 ± 0.22	0.22 ± 0.13	0.299	5.966	.7749
1 m CT <sub>MAX</sub>	38.20 ± 1.13	40.93 ± 4.23	-1.097	2.173	.3794

Note: TPC were estimated by fitting the beta equation to running speed across 20 cm (mean fastest) and 1 m (mean) distances at five temperatures. Values in the "Male" and "Female" columns are mean ± SD for each measure (°C for all but W<sub>f</sub> which is m/s).

Abbreviations: CT<sub>MAX</sub>, critical thermal maximum; PBT, preferred body temperature; SD, standard deviation; T<sub>OPT</sub>, optimum temperature where performance is maximized; T<sub>SET</sub>, thermal set-point range; TPC, thermal performance curve; VT<sub>MAX</sub>, voluntary thermal maximum; VT<sub>MIN</sub>, voluntary thermal minimum; W<sub>f</sub>, peak performance.

measures, neither T<sub>OPT</sub> nor CT<sub>MAX</sub> differed between measures, although peak performance (W<sub>f</sub>) was 0.19 m/s faster (73%) for mean fastest sprint speed than mean 1 m speed (Table 4). Pooled across measure, age class, and sex, T<sub>OPT</sub> was 32.19 ± 3.49°C and CT<sub>MAX</sub> was 39.94 ± 4.07°C (Figure 1b). The lower and upper T<sub>d</sub> where the TPC deviated from an exponential pattern were 28.31°C and 36.06°C, respectively.

During the austral summer (December–February), the average minimum daily air temperature (±SD, i.e., nighttime low) from 1989 to 2009 in Noumea, New Caledonia, was 23.1 ± 0.8°C and ranged from 17.8°C to 27.2°C (Figure 2). Average maximum daily air temperature (i.e., afternoon high) for this same period was 29.5 ± 0.6°C and ranged from 22.1°C to 36.4°C (Figure 2). Thus, the average conditions throughout the summer remained within the voluntary thermal limits for activity and temperatures within T<sub>SET</sub> were readily available, particularly at night when crested geckos are most active (Figure 2).

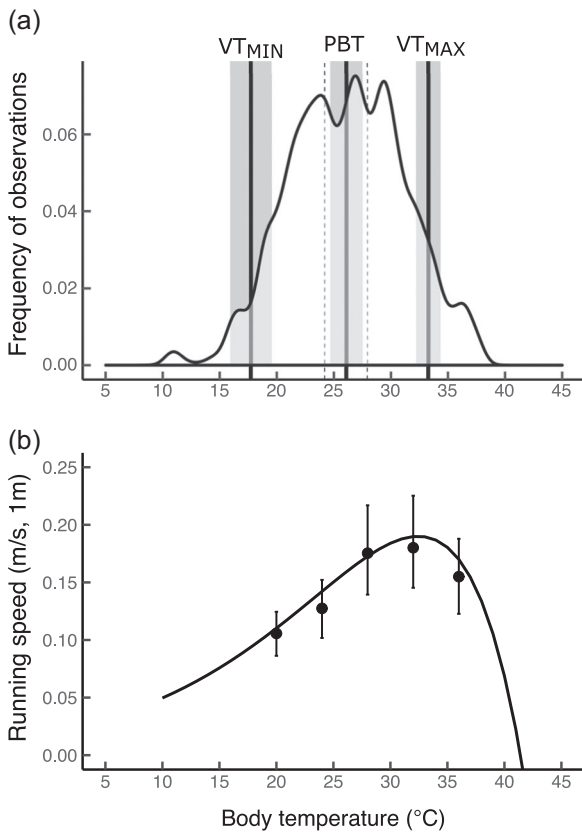
## 4 | DISCUSSION

Because of their differences in size, ontogenetic stages frequently occupy different ecological niches and experience different selection pressures (Bowler & Terblanche, 2008; Werner & Gilliam, 1984). However, such differences do not appear to have affected the evolution of thermal behavior or tolerance in crested geckos. Both thermoregulatory behavior and TPCs were highly conserved among age classes, with no measure affected by age class, despite adults being an order of magnitude larger than juveniles (mean mass ± SD = 30.5 ± 9.1 and 4.0 ± 1.6 g for adults and juveniles, respectively). Moreover, age classes did not differ in either their mean fastest 20 cm sprint speed or mean 1 m running speed. These similarities

**TABLE 3** Results from Welch's two-sample t tests comparing measures of thermoregulatory behavior and TPC parameters among adult male and adult female crested geckos, *Correlophus ciliatus*

suggest that size-driven differences between age classes in competitive ability or access to microenvironments have not resulted in the evolution of stage-specific thermal biology or running performance in these lizards.

The thermal biology of crested geckos appears well suited to their natural environment in New Caledonia, despite our measurements being on animals that spent multiple generations in captivity. During the active season, nighttime air temperatures between 1989 and 2009 in New Caledonia were almost always within the T<sub>SET</sub> range, and air temperatures remained within voluntary thermal limits year-round for most of the day. When temperature was outside T<sub>SET</sub> at night, it generally was below T<sub>SET</sub>, especially in winter. As a result, climate change-induced temperature increases will likely be beneficial for crested geckos, allowing increased daily and seasonal activity. However, our confidence in this conclusion hinges on the assumption that captive-reared individuals have thermal biology representative of wild animals. To date, no published data on the thermal ecology of wild crested geckos are available but researchers working with *C. ciliatus* in the field tell us that field body temperatures correspond well to a T<sub>SET</sub> of 24–28°C (A. M. Bauer [personal communication, July 26, 2019]), and geckos have done best in captivity when maintained from 25°C to 28°C ever since their rediscovery (de Vosjoli, 2005; de Vosjoli & Repashy, 2014; Team, 2017). Additionally, there are multiple conceptual reasons to expect a similar thermal biology between captive and wild crested geckos. First, thermal traits other than critical minima tend to be highly conserved among reptile populations, even for widespread species (Angilletta, Zelic, Adrian, Hurliman, & Smith, 2013; Buckley, Ehrenberger, & Angilletta, 2015; Muñoz et al., 2016, but see Gilbert & Miles, 2019 for an exception). Crested geckos, by contrast, are not widespread, and presumably have small population sizes (Bauer & Sadlier, 2000).



**FIGURE 1** Comparison of (a) thermoregulatory behavior and (b) thermal performance in crested geckos, *Correlophus ciliatus*. Data from adults and juveniles are pooled because parameters did not differ by age class (Tables 1 and 2). For (a), the density plot shows the frequency of body temperatures maintained by lizards on a laboratory thermal gradient. Means and 95% confidence intervals for the  $VT_{MAX}$ ,  $VT_{MIN}$ , and PBT are shown via solid vertical lines and shaded regions. Estimated  $T_{SET}$  is illustrated with vertical dashed lines around PBT. For (b), dots and whiskers are mean 1 m running speed and 95% confidence limits at five test temperatures. The curved line is the average thermal performance curve fit to these data. The peak of this curve is  $T_{OPT}$  and the high temperature where the curve crosses the x axis is  $CT_{MAX}$ . The x axes on both plots have the same scale allowing direct visual comparison of thermal behavior and performance. PBT, preferred body temperature;  $T_{OPT}$ , optimum temperature where performance is maximized;  $T_{SET}$ , thermal set-point range;  $VT_{MAX}$ , voluntary thermal maximum;  $VT_{MIN}$ , voluntary thermal minimum

Thus, additive genetic variation is likely small, greatly limiting the capacity for evolution in the wild and minimizing potential founder effects in captive populations. Additionally, crested geckos have only been maintained in captivity since the mid-1990s (~25 years, de Vosjoli, 2005), allowing ~16 generations (assuming an 18-month generation time; Bauer & Sadlier, 2000) which is a short time for captive evolution. Thus, genetic differences in thermal biology between captive and wild populations is likely minimal, although differences due to acclimation and phenotypic plasticity could still be important (Ballinger & Schrank, 1970; Pintor, Schwarzkopf, & Krockenberger, 2016; Taylor et al., 2020).

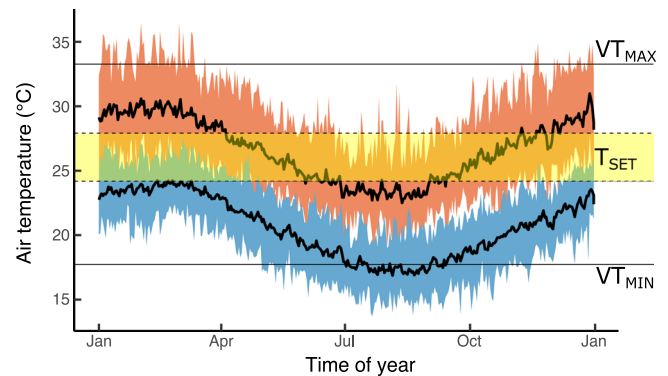
**TABLE 4** Results from Welch's two-sample *t* tests comparing TPC parameters between two performance measures (mean fastest 20 cm sprint speed and mean 1 m running speed) in crested geckos, *Correlophus ciliatus*

Measure	20 cm speed	1 m speed	<i>t</i> value	<i>df</i>	<i>p</i> value
$T_{OPT}$	31.96 ± 4.07	32.46 ± 2.71	-0.51	43.79	.6151
$W_f$	0.45 ± 0.26	0.26 ± 0.17	3.05	43.35	<b>.0039</b>
$CT_{MAX}$	40.34 ± 4.85	39.47 ± 2.94	0.76	42.03	.4503

Note: Data are pooled across age classes which did not differ (Table 3). TPCs were estimated by fitting the beta equation to running speed at five temperatures. Values in the “20 cm speed” and “1 m speed” columns are means for each measure (°C for  $T_{OPT}$  and  $CT_{MAX}$ , m/s for  $W_f$ ). Bold value is statistically significant (i.e.,  $p < .05$ ).

Abbreviations:  $CT_{MAX}$ , critical thermal maximum;  $T_{OPT}$ , optimum temperature where performance is maximized;  $W_f$ , peak performance.

In the pet trade, crested geckos are especially popular because they perform well in human homes without additional heating or lighting requirements (de Vosjoli, 2005). However, our results suggest that crested geckos have a fairly typical thermal biology for a lizard. When provided a thermal gradient, they actively thermoregulate to within a 3–4°C set-point range and their running performance is affected by temperature similar to other species (Huey, 1982; Ivey et al., 2020; Muñoz et al., 2016; Tomlinson, 2019). Although the preferred and optimal temperatures of crested geckos are below those of many diurnal, heliothermic species, they are very



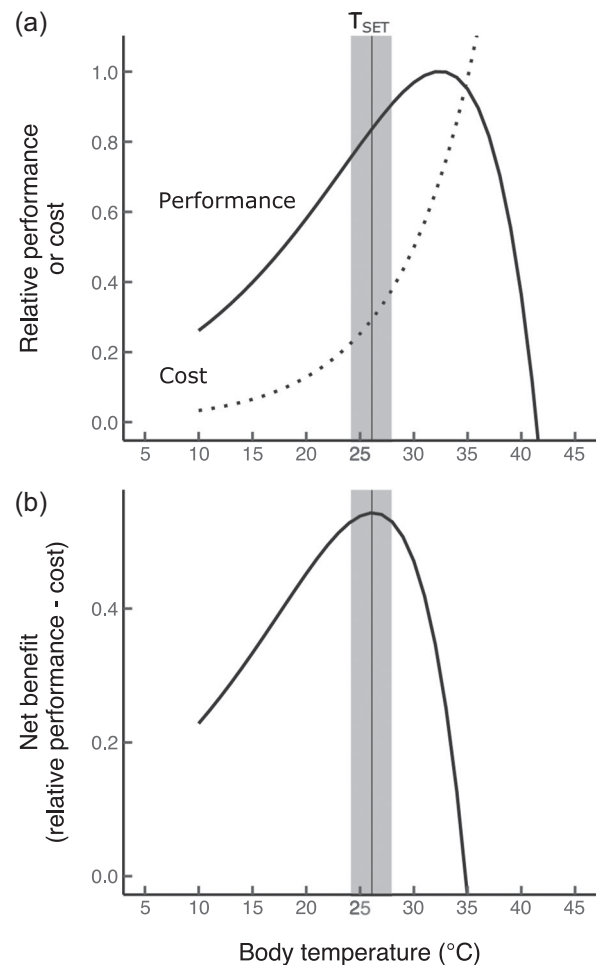
**FIGURE 2** During the austral summer (December–March) nighttime air temperatures are typically within the  $T_{SET}$  range for crested geckos, *Correlophus ciliatus*, and air temperatures remain within voluntary thermal limits throughout much of the year. The upper bold line surrounded by shading (red online) is mean ± range of daily maximum temperature from 1989 to 2009, whereas the lower bold line and shaded region (blue online) is mean ± range of daily minimum temperature for this period. Data are from a weather station in Noumea, New Caledonia. Overlaid are estimates of thermoregulatory behavior for *C. ciliatus* in the laboratory including  $VT_{MAX}$  and  $VT_{MIN}$  (solid horizontal lines) and the  $T_{SET}$  range (horizontal shaded region bounded by dashed lines, yellow online). Voluntary limits and  $T_{SET}$  are the same as in Figure 1a.  $T_{SET}$ , thermal set-point range;  $VT_{MAX}$ , voluntary thermal maximum;  $VT_{MIN}$ , voluntary thermal minimum [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

similar to estimates for other nocturnal and shade-dwelling species (Brown, 1996; Muñoz et al., 2016; Telemeco et al., 2017). Thus, the lack of special heating requirements for crested geckos maintained as pets does not result from these geckos being thermal generalists, but rather their thermal biology aligning with temperatures commonly maintained in human homes.

#### 4.1 | Comparing performance and behavior: An extended optimality hypothesis for the evolution of thermal set-points

Unlike what we might expect from classic theory (reviewed in Angilletta, 2009), PBT and  $T_{OPT}$  did not overlap in crested geckos. Rather,  $T_{OPT}$  for running was 6.1°C higher than PBT and 4.3°C higher than the upper  $T_{SET}$  limit. As a result,  $T_{OPT}$  aligned with  $VT_{MAX}$  (Figure 1). PBT estimates substantially below  $T_{OPT}$  estimates are common in reptiles and other ectotherms. Potential explanations for this discrepancy include selection acting to match PBT with alternative performance measures or an average of all performance measures, or selection acting to reduce the risk of overheating rather than maximize performance (Angilletta, 2009; Huey & Bennett, 1987; Martin & Huey, 2008).

Intriguingly, PBT in crested geckos closely aligned with their lower threshold temperature (lower  $T_d$ ). Although the lower and upper  $T_d$  are infrequently estimated, evidence to date suggests PBT might commonly align with the lower  $T_d$  in lizards (Tomlinson, 2019), and this observation suggests a third, nonmutually exclusive, optimality hypothesis for how selection acts to set PBT (Figure 3). Because the lower  $T_d$  is the temperature where the TPC begins to deviate from an exponential-up pattern (Tomlinson, 2019), performance increases less rapidly above the lower  $T_d$  than below the lower  $T_d$ , with increases dropping to zero at  $T_{OPT}$  (i.e., the derivative of the TPC drops from its maximum to zero between the lower  $T_d$  and  $T_{OPT}$ ). If we think of performance as a benefit, this means that organisms receive diminishing returns when their body temperatures rise above the lower  $T_d$  although they continue to experience increased costs of ever-increasing metabolic demand and overheating risk (Figure 3a). Thus, the optimum body temperature where the performance benefit most outweighs associated costs (i.e., greatest net benefit) should approximate the lower  $T_d$  (Figure 3b).  $VT_{MAX}$  coinciding with  $T_{OPT}$  is also explained by this optimality hypothesis because the net benefit should approach zero at  $T_{OPT}$  and become negative between  $T_{OPT}$  and  $CT_{MAX}$ , at approximately the upper  $T_d$  (Figure 3b). Unlike the model of Martin and Huey (2008), this hypothesis does not rely on TPC asymmetry and Jensen's inequality to explain selected body temperatures below  $T_{OPT}$ , and both mechanisms could simultaneously influence PBT evolution. The key assumption of our extended optimality hypothesis is that costs increase exponentially with body temperature, which is plausible given that metabolic demand increases exponentially. Still, further exploration of the costs and benefits associated with maintaining body temperature above and below the lower  $T_d$ , and further estimation of both  $T_d$  in



**FIGURE 3** Schematic illustration of an optimality approach to understanding the evolution of thermoregulatory set-points. Under this framework, animals are hypothesized to be under selection to maintain body temperatures that maximize net performance benefits (i.e., maximize running performance while minimizing associated costs), which should occur at the lower  $T_d$ , the body temperature where the TPC deviates from an exponential-up pattern. (a) TPC for 1 m running speed in crested geckos (*Correlophus ciliatus*) represented as a solid black line, with performance scaled such that  $W_f = 1$ . Overlaid is a hypothetical cost curve (dotted line) encompassing the effects of body temperature on both metabolic demand and overheating risk. An exponential cost curve is assumed because metabolic demand increases exponentially with temperature while the risk of overheating should increase linearly. (b) The effect of body temperature on net benefits resulting from the cost and benefit curves in (a). The  $T_{SET}$  range (vertical shaded region) and PBT (vertical line) for *C. ciliatus* is overlaid on both plots for reference and are the same as in Figure 1a. PBT, preferred body temperature;  $T_d$ , temperature of deviation from exponential;  $T_{SET}$ , thermal set-point range; TPC, thermal performance curve;  $W_f$ , peak performance

additional species are needed to directly test this optimality hypothesis for the evolution of thermoregulatory set-points in reptiles.

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## DATA AVAILABILITY STATEMENT

All data for this study are available as online supporting information.

## ORCID

Rory S. Telemeco  <http://orcid.org/0000-0002-0767-8565>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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