ORIGINAL RESEARCH

Ecophysiological trait variation in desert versus Mediterranean populations of a gecko

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Keywords

Abstract

arid; ectotherm; evaporative water loss; intraspecific; mesic; metabolic rate; morphology; temperature preference.

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Populations inhabiting several biomes may experience different abiotic and biotic conditions, exerting local selection pressures. Temperature and water regimes are interconnected variables, that may differ between biomes, and greatly influence ecophysiological traits, such as metabolic and evaporative water loss rates. We hypothesized that Ptyodactylus guttatus (Sinai Fan-fingered Gecko) individuals, which occupy the Mediterranean and desert biomes across Israel, would follow the "metabolic cold adaptation" hypothesis and be adapted to the microclimate in the biome they inhabit. We thus predicted that desert individuals would prefer lower temperatures, and have lower resting metabolic rates and evaporative water loss rates at higher ambient temperatures than Mediterranean individuals. We also predicted that Mediterranean individuals would have a better body condition than individuals from the desert, because of higher primary productivity in the Mediterranean biome, and would therefore have higher mite loads. We further predicted that geckos from the desert would have longer limbs, enabling them to lose more heat to the environment, according to Allen's rule. To test these hypotheses, we measured the temperature preferences, field body temperatures, resting metabolic rates, evaporative water loss rates, body conditions, mite loads, and limb lengths of 82 P. guttatus individuals collected from four localities two from the desert biome and two from the Mediterranean biome. There were no significant differences in any of the tested traits when comparing between biomes. However, we found some differences in the evaporative water loss rates, body temperatures, body condition, and forelimb lengths between the northernmost and southernmost, and driest and wettest localities, supporting some of our predictions. Our results highlight the importance of the resolution of the analysis. Although some ecophysiological traits of P. guttatus seem to be conserved across localities and biomes, thermal plasticity in these traits may have helped this species reach its current distribution and occupy two biomes.

Introduction

Species with wide geographical distributions may experience different environmental conditions throughout their range (Pincheira-Donoso & Meiri, 2013; Prates et al., 2022). Different abiotic and biotic conditions across the range of species may exert different selection pressures on ecophysiological characteristics (Smith & Ballinger, 2001; Titon Jr & Gomes, 2017). The distribution of a species may also dictate its trait variation and potential for adaptation to different conditions (Grinnell, 1917; Kearney et al., 2013; Orr & Smith, 1998; Riddell et al., 2017). Thus, adaptation and distribution may

interact through the evolutionary history of species (Morrison et al., 2012). Temperature and precipitation regimes are two important interconnected abiotic variables that may differ greatly between biomes and may have great influence on species' life history traits, activity patterns and survival (Herrando-Pérez et al., 2020; Pirtle et al., 2019; Rozen-Rechels et al., 2020). Ectotherms rely mostly on selection of microenvironments with different temperatures to regulate their body temperature, thereby affecting important physiological processes such as metabolic rate and water balance (Belasen et al., 2017; Crowley, 1987; Dubiner et al., 2023; Killen, 2014; Killen, 2014;

Plasman et al., 2020). The 'metabolic cold adaptation' hypothesis claims that when placed in the same ambient temperature, ectotherm species, or populations, inhabiting cold habitats have higher metabolic rates compared with conspecifics from warm habitats (Chown & Gaston, 1999; Krogh, 1914). According to this hypothesis, this compensates for the fact that biochemical processes are slower in lower temperatures (Tattersall et al., 2012; Abram et al., 2017). Maintaining higher metabolic rates enables ectotherms to maintain high levels of development, growth, activity, and reproduction, despite shorter daily or seasonal warm periods in cold climates (Clarke, 1991, 2004; Scholander et al., 1953). Additionally, lowering metabolism in warm and dry climates can lead to lower respiratory and cutaneous water loss, thereby reducing the total evaporative water loss and conserving water (Mautz, 1982; Woods & Smith, 2010). Species from arid habitats have been found to have significantly lower evaporative water loss rates, compared with those from mesic habitats (Cox & Cox, 2015; Mautz, 1982), mainly due to the evolution of mechanisms reducing excessive cutaneous and respiratory water loss (Hlubeň et al., 2021). These include the development of thicker body and ocular scales, increasing the resistance of the scales and skin to evaporation, reducing space between scales, and lowering metabolic rates, hence also breathing rates and the associated loss of water they entail (Broeckhoven et al., 2018; Dmi'el, 1998, 2001; Eynan & Dmi'el, 1993; Hlubeň et al., 2021; Mautz, 1982; Oufiero & Van Sant, 2018; Woods & Smith, 2010).

The preferred body temperature of ectotherms is thought to be correlated with the optimal temperature of many physiological processes and performance (Angilletta Jr. et al., 2002; Angilletta Jr., 2009; Bauwens et al., 1995; Huey & Bennett, 1987; Oliveira et al., 2022). While the preferred body temperatures tend to be conserved across species (Van Damme et al., 1990) and populations inhabiting different environmental conditions (Carretero et al., 2005; Gvozdík & Castilla, 2001; Van Damme et al., 1989, 1990), there is still substantial interand intraspecific variation (Bauwens et al., 1995). But ectotherm preferred body temperatures are affected by additional factors (Rozen-Rechels et al., 2019). The hydration state has been found to influence ectotherm preferred body temperatures (Ladyman & Bradshaw, 2003; Preest & Pough, 1989; Rozen-Rechels et al., 2019) and thereby performance (Anderson & Andrade, 2017; Preest & Pough, 1989; Rozen-Rechels et al., 2019). Basking in hot and dry environments exposes ectotherms to heat and dry air, resulting in an increased metabolic rate (Christian & Bedford, 1995; Krawchuk & Brooks, 1998). This, in turn, increases evaporative water loss (Lillywhite et al., 1998; Sinsch, 1989; Withers & Thompson, 2000). Temperature selection can therefore affect both activity levels and water balance (Ladyman & Bradshaw, 2003). Low body temperature, and reduced activity levels, will also decrease water loss, mainly by decreasing respiratory water loss, a decrease that can be beneficial for desert inhabitants (Mautz, 1982). Ectotherms inhabiting colder environments may have to spend more time and energy on thermoregulation than in warmer habitats (Grbac & Bauwens, 2001; Gvoždík, 2002; Huey, 1982). In cold environments ectotherms will have less

time for other activities, such as foraging, mating, and avoiding predators (Huey, 1982; Huey & Slatkin, 1976). This is unless they adapt to perform well in lower temperatures by, for example, shifting their thermal performance curve, and their preferred temperature along with it, to lower temperatures (Bodensteiner et al., 2021).

The temperature and humidity of a habitat may influence the activity level and reproductive success of parasites (Pollock et al., 2015), that, in turn, can negatively affect host body condition (Cook et al., 2013; Dunlap & Mathies, 1993; Klukowski & Nelson, 2001). Various mechanisms have been proposed to explain the relationships between ectoparasite load, body condition, and physiological responses of infected lizards in different habitats (Conover et al., 2015; Sannolo et al., 2020). For instance, it has been suggested that lizards increase their body core temperatures through increased basking, creating a behavioral fever, to cause ectoparasites to drop off, or to combat internal pathogens transmitted by those ectoparasites (Conover et al., 2015). The cutaneous water loss of lizards from cold climates was also suggested to be lower due to reduced superficial blood flow and capillary structure caused by heavy ectoparasite load (Sannolo et al., 2020). The effects of ectoparasites on host physiology and body condition, and the mechanisms by which lizard species and populations cope with parasite infestation in different climates and habitats, are still poorly understood. Limb morphology may also vary according to climatic conditions (Mayr, 1963). In endotherms, longer protruding body parts, such as ears, tails, and limbs are often correlated with warmer climates, a pattern known as 'Allen's Rule' (Allen, 1877; Ryding et al., 2021; Symonds & Tattersall, 2010). Longer extremities increase the body surface area to body volume ratio, and thereby enable higher heat loss among species occupying hotter environments (Ray, 1960). Several Israeli desert lizard species have been found to have longer legs than Mediterranean species (Izhaki & Haim, 1996; Volynchik, 2014). But whether this rule is valid in ectotherms in general, and in lizards in particular, is still debated (Alho et al., 2011; Jin et al., 2006; Jin & Liao, 2015; Liang & Shi, 2017; Norris et al., 2021; Zhao et al., 2020).

Many studies compare traits of different species from the same habitat (e.g., Arad et al., 1989; Muñoz-Nolasco et al., 2019) or several phylogenetically close species occupying different biomes (Arad et al., 1989; Clemente et al., 2009; Dmi'el, 1998; Eynan & Dmi'el, 1993; Fehrenbach, 2017; Herrando-Pérez et al., 2020; Hlubeň et al., 2021; Mautz, 1982). Fewer studies explore the intra-specific variation of wideranging species occupying several habitats or biomes (but see Araya-Donoso et al., 2022; Belasen et al., 2017; Cooper et al., 2018; Kirchhof et al., 2017; Klüg-Baerwald & Brigham, 2017). Understanding the intra-specific variation in physiological characteristics in arid and mesic environments is crucial to comprehending the intricate connections between animals and their environments, how those affect their ranges, and the processes that shape them. Studying intra-specific ecophysiological traits may also be vital in order to assess the future ramifications of globally rising temperatures, which can potentially cause local extinctions and range reduction or expansion (Deutsch et al., 2008; Dupoué et al., 2017; Herrando-Pérez et al., 2020; Kearney, 2013; Kearney et al., 2013; Kirchhof et al., 2017; Sinervo et al., 2010; Stark et al., 2023). It can also benefit conservationists in conducting recovery actions, such as translocations or reintroductions (Besson & Cree, 2010; Cooper et al., 2018; Tarszisz et al., 2014), and in assessing the abilities of species to facilitate invasion of new habitats (Kolbe et al., 2014; Lapwong et al., 2020).

Israel includes two main biomes: a Mediterranean and a desert biome (Olson et al., 2001). The Mediterranean biome is characterized by cool and wet winters, and hot and dry summers. The desert biome experiences extreme temperature differences between day and night, and less than 250 mm annual rainfall (Fick & Hijmans, 2017). The cathemeral, insectivorous, rupicolous scansorial Sinai fan-fingered gecko (Ptvodactylus guttatus; Heyden, 1827; Squamata: Phyllodactylidae) occupies both the Mediterranean biome in the north (the species' northernmost range edge), and the desert biome up to Eilat in the south (Bar et al., 2021; Roll et al., 2017). Throughout its distribution, P. guttatus, similarly to its congeners, can be found on large rocks, boulders or rock-walls, and human-made substrates (Metallinou et al., 2015). Previous studies, which examined this species throughout its global range, did not find substantial genetic substructuring in the species (Metallinou et al., 2015). Earlier studies, however, found evidence for intra-specific variation in some morphological and physiological characteristics throughout its distribution in Israel, especially in the border areas where they are sympatric with P. hasselquistii in the south and P. puiseuxi in the north (Arad et al., 1989; Werner & Sivan, 1993), but no systematic variation in body size (Pincheira-Donoso & Meiri, 2013).

We examined whether P. guttatus populations from the desert and Mediterranean biomes differ in their temperature preferences, metabolic rates, respiratory water loss and morphology. We hypothesized that P. guttattus follow the "metabolic cold adaptation" hypothesis and are adapted to the microclimate at the habitat they inhabit. Thus, we predicted that geckos from the hot and arid desert would be better adapted to hotter, drier conditions while geckos from cooler and more humid Mediterranean environments would be better adapted to lower temperatures and higher water availability. Specifically, we predicted that desert individuals would prefer lower body temperatures than Mediterranean ones. That would allow them to lower their metabolic rate and lose less water as a consequence (Woods & Smith, 2010). Additionally, we predicted that if geckos indeed adapted to the microclimate in the places they inhabit, their body temperatures, measured in the field upon capture, would be similar to those measured in the laboratory at the same time of day. We also predicted that, in the same higher ambient temperatures, geckos from the desert would have lower resting metabolic rates (as has been found across species of squamates in Israel; Dubiner et al., 2023), and respiratory water loss, compared with geckos from the Mediterranean biome. Additionally, we predicted that evaporative water loss would be lower in geckos which have a higher ectoparasite load. In this case, if the ectoparasite load on geckos from the Mediterranean biome is higher than that of geckos from the desert, the former may have lower water loss rates than desert individuals because heavy ectoparasite load

may cause reduced superficial blood flow and capillary structure, thereby reducing cutaneous water loss of lizards from cold climates (Sannolo et al., 2020). Furthermore, we predicted that because in the Mediterranean biome the primary productivity is higher than in the desert (Hadley & Szarek, 1981), Mediterranean geckos would have a better body condition (resulting from higher fat reserves) than desert geckos (Rosenzweig, 1968). This would hold unless geckos from the Mediterranean biome have higher ectoparasite loads, which in turn, would negatively affect their body condition (Cooper et al., 1985; but see Bull & Burzacott, 1993). Finally, we predicted that geckos from the desert would have longer limbs than geckos from the Mediterranean biome, in accordance with Allen's rule.

Materials and methods

Study sites

Two of the study sites we sampled belong to the desert biome (Nahal Atadim and Nahal Ze'elim), and two to the Mediterranean biome (Hurbat Burgin and Nahal Oren; Fig. 1). These sites differ in their latitude (Table 1), temperatures, and precipitation (Table S1). The southernmost site, Nahal Atadim (31.06° N, 34.78° E), is located in the Negev Desert in Southern Israel, and is part of the Saharo-Arabian Desert (Gutterman, 2001). It receives ~ 100 mm average rainfall annually, with $\sim 60\%$ annual relative humidity and mean annual temperatures of 20 °C (HaNegev Junction weather station; the Israel Meteorological Service archive; Table S1). The second desert site, Nahal Ze'elim (31.35° N, 35.36° E), is located in the Judean Desert, a rain-shadow desert resulting from a steep drop of ~ 1200 m from the Judean mountains (~ 800 m above sea level) to the lowest point on Earth, the Dead Sea $(\sim -430 \text{ m} \text{ below sea level})$. It receives $\sim 50 \text{ mm}$ rainfall annually, has 42% mean annual relative humidity and a mean annual temperature of $\sim 27^{\circ}$ C, with temperatures easily exceeding 45°C during the hottest months (July-August; Ein Gedi weather station; the Israel Meteorological Service archive; Table S1). The southern Mediterranean biome locality we sampled in, Hurbat Burgin (=Burgin Ruins; 31.64° N, 34.97° E), is located in the Judean Plains, between the Judean Mountains and the Coastal Plain. With mean annual temperatures of $\sim 20^{\circ}$ C, it receives, on average, ~ 450 mm of rainfall annually and has a mean relative humidity of 60% (Beit Jamal weather station; the Israel Meteorological Service archive; Table S1). The mean annual temperatures in Nahal Oren (32.71° N, 34.97° E), the northern Mediterranean locality, are $\sim 20^{\circ}$ C, with a mean relative humidity of 70% and it receives on average ~600 mm of rainfall annually (Ein Carmel weather station; the Israel Meteorological Service archive; Table S1).

Data collection

We collected 82 *P. guttatus* individuals of both sexes (35 females, 47 males) from four locations in Israel (Nahal Oren: n = 21, Hurbat Burgin: n = 17, Nahal Ze'elim: n = 16, Nahal Atadim: n = 17; Fig. 1, Table S2) between March–September



Figure 1 Map of Israel with the Mediterranean (green) and desert (yellow) biomes, indicating the localities from which geckos were collected. Nahal Atadim (31.06 N, 34.78 E; yellow star) and Nahal Ze'elim (31.35 N 35.36 E; red triangle) are in the desert and Nahal Oren (32.71 N, 34.97 E; blue square) and Hurbat Burgin (31.64 N, 34.97 E; green circle) are in the Mediterranean biome.

2019 and June 2020 under permits no. 2018/42082 and 2019/ 42284 issued by the Israel Nature and Parks Authority. The geckos were located by sight on walls, boulders, and rocks, and were caught by hand or with a noose. Most individuals were caught in the morning (Nahal Oren: 07:30–11:30; Hurbat Burgin: 07:30–09:30; Nahal Ze'elim: 06:15–09:00; Nahal Atadim: 08:00–11:00; Table S2), because these are the times in which this species is most active (Schwarz et al., 2021). For logistical reasons, in three localities, few individuals were also collected in the afternoon (Nahal Oren: 13:00–15:00, 3 individuals) and evening (Hurbat Burgin: 18:20–19:20, 6 individuals; Nahal Ze'elim: 19:30–20:30, 8 individuals; Table S2). All geckos were released at the point of capture after the end of the experiments.

Upon capture, we measured the body temperature of each individual using a cloacal probe attached to a K-type thermometer (Hyelec[®] MS6501) to the nearest 0.1° C. After capture, geckos were housed individually in $460 \times 300 \times 170$ mm transparent plastic terraria (Exo Terra[®] PT2310 faunarium) for habituation to lab conditions (25°C) at the Zoological Research Garden at Tel Aviv University. Terraria were supplemented with heating lamps, and geckos provided twice a week with

Locality				
Trait	Nahal Oren	Hurbat Burgin	Nahal Atadim	Nahal Ze'elim
Biome	Mediterranean	Mediterranean	Desert	Desert
Collection site coordinates	32.71° N, 34.97° E	31.64° N, 34.97° E	31.06° N, 34.78° E	31.35° N, 35.36° E
Mass [g]	$12.8 \pm 0.4 \ (n = 21)$	$8.8 \pm 0.3 \ (n = 17)$	$10.0 \pm 0.4 \ (n = 17)$	$7.3 \pm 0.3 (n = 16)$
SVL [mm]	74.6 \pm 0.7 (<i>n</i> = 21)	$69.1 \pm 0.6 \ (n = 17)$	$69.4 \pm 0.7 \ (n = 17)$	$65.1 \pm 0.6 \ (n = 16)$
Mean forelimb length [mm]	$25.0 \pm 0.2 \ (n = 21)$	$24.3 \pm 0.2 \ (n = 17)$	$25.1 \pm 0.2 \ (n = 17)$	$23.9 \pm 0.2 \ (n = 16)$
Mean hind limb length [mm]	$31.1 \pm 0.3 (n = 20)$	$30.3 \pm 0.3 \ (n = 17)$	30.8 ± 0.3 (n = 17)	$29.4 \pm 0.3 \ (n = 16)$
Mean O_2 consumption rate at 35°C [mL x min ⁻¹]	0.032 ± 0.004 (n = 14)	0.031 ± 0.003 (n = 16)	0.033 ± 0.004 (n = 12)	0.022 ± 0.002 (n = 14)
Mean O_2 consumption rate at 25°C [mL x min ⁻¹]	0.015 ± 0.002 (n = 14)	$0.019 \pm 0.002 \ (n = 16)$	$0.018 \pm 0.002 \ (n = 12)$	$0.013 \pm 0.002 \ (n = 14)$
Mean evaporative H_2O loss at 35°C [μ L × h ⁻¹]	6.96 ± 0.27 (<i>n</i> = 15)	8.70 ± 0.88 (n = 16)	9.02 ± 1.11 (n = 11)	7.61 ± 1.13 (<i>n</i> = 13)
Mean evaporative H ₂ O loss at 25°C $[\mu L \times h^{-1}]$	4.91 ± 0.78 (<i>n</i> = 15)	$3.00 \pm 0.63 \ (n = 16)$	3.89 ± 0.80 (n = 11)	2.68 ± 0.65 (n = 13)
Mean preferred body temperature [°C]	$32.3 \pm 0.4 \ (n = 21)$	$33.0 \pm 0.3 \ (n = 16)$	34.0 ± 0.2 (n = 15)	$33.3 \pm 0.2 \ (n = 16)$
Mean interquartile range (Q1–Q3) of preferred body temperatures distribution [°C]	30.2–34.6	31.65–34.4	33.1–35.2	32.2–34.7
Mean field body temperature [°C]	$21.0 \pm 1.4 (n = 16)$	$28.4 \pm 0.6 (n = 15)$	$28.5 \pm 0.5 (n = 15)$	$34.0 \pm 1.2 \ (n = 9)$
Mean field substrate temperature [°C]	$19.3 \pm 0.8 (n = 29)$	$27.3 \pm 0.7 (n = 16)$	$27.2 \pm 0.4 (n = 17)$	$35.5 \pm 1.3 (n = 6)$
Mean field air temperature [°C]	$18.6 \pm 0.7 \ (n = 29)$	$26.8 \pm 0.6 \ (n = 16)$	$27.1 \pm 0.4 \ (n = 17)$	$35.7 \pm 1.1 \ (n = 6)$

Table 1 Mean values of ecophysiological and morphological traits measured in the field and from experiments performed on *Ptyodactylus* guttatus collected from four localities situated in the Mediterranean and desert biomes in Israel

Each mean is presented with its standard error and the n on which it is based.

mealworms, and water ad lib. Vitamin and mineral supplements were administered twice a month. We removed leftover mealworms from enclosures 48 h before initiation of each measurement, and provided geckos with fresh mealworms after finishing each experiment. To exclude the effects gravidity may have on the preferred temperatures and metabolic rates (Carretero et al., 2005) we did not perform experiments on gravid females, but waited until they laid the eggs. Geckos rested at least 72 h between experiments. We performed the following experiments at least 7 days, and no later than 8 months, after capture (Table S2).

Resting metabolic rate and evaporative water loss measurements

Resting metabolic rate and evaporative water loss were measured using flow-through respirometry in a push mode (following Lighton, 2018). We measured the metabolic rate for a total of 58 geckos. For each measurement, seven geckos (deprived of food for 72 h before the test) were placed in individual 60 mL plastic metabolic chambers where geckos were constrained but not prevented from voluntary movement. We observed that their ventral side was not in permanent contact with the metabolic chamber, as geckos supported themselves on their feet. Metabolic chambers were placed inside a temperature-controlled cabinet (Panasonic, Japan), set at 25 or 35°C, and left to acclimate for 1 h in the temperaturecontrolled cabinet, inside the metabolic chambers, before the onset of measurement. Each gecko was tested twice, in cycles, once in each temperature, with no less than 3 days between trials. We used eight-channel multiplexers (Sable Systems, Las Vegas, Nevada) to measure seven individuals consecutively for two 20-min recordings each time. An empty cell was used as a baseline reference and was measured for 10 min every 40 min (every two cycles). Atmospheric air was dried of water and absorbed from CO₂ by passing through a column of magnesium perchlorate (water absorbent) and Ascarite[®] (CO₂ absorbent), and it then flowed at a rate of 50 mL $\times\mbox{min}^{-1}$ (Clemente et al., 2009; Cohen et al., 2022; V8, eight-channel flow mass control, Sable Systems, Las Vegas, Nevada) into each metabolic chamber. Air exiting the chambers passed through a Li-7000 CO₂/H₂O analyzer (Licor, Lincoln, Nebraska, USA) and then through a column of magnesium perchlorate and Ascarite[®] (water and CO₂ adsorbents, respectively) into an O2 analyzer (Oxzilla II, Sable Systems, Las Vegas, Nevada). A baseline of 5 min was run at the beginning and the end of a recording session, and after every two samples, and served for drift correction. At the end of each measurement, we recorded the mass of each individual with an analytic balance (to 0.01 g, Sartorius, Quintix, Germany). We failed to weigh nine individuals after their measurement in 35°C because the analytic balance malfunctioned. Therefore, we used the mass measured for these individuals after measurement in 25°C (difference in masses between sessions for other geckos never exceeded 1.5 g; Table S2).

Data acquisition and analyses were carried out using Expe-Data software (Sable Systems International, Las Vegas, NV, USA). Resting metabolic rates were estimated for each

individual as the mean values of the lowest and most level 10min samples out of two cycles of 20-min data recordings. If an individual was observed moving (by detecting high fluctuations in VCO₂ or by direct observation through the metabolic chamber) or defecating (feces found inside metabolic chamber after measurement), we disregarded that measurement. The VO₂ was calculated by ExpeData software, using the equation in Lighton (2018):

$$VO_2 = FR_i(F_iO_2 - F_eO_2)/(1 - F_eO_2)$$

where FR_i is the flow rate through the metabolic chamber, F_iO_2 refers to the fraction of O_2 in air running through the chamber, and F_eO_2 is O_2 fraction at the exit of the chamber. Evaporative water loss was calculated by integrating (over hours) the area under the H₂O recording curve of the lowest level for a 5-min period out of two 20-min recording periods. EWL was corrected using a linear calibration curve that was created by injecting microliter amounts of water into a stream of CO₂-free dry air passing through the empty metabolic chamber under the two different experimental temperatures, and integrating the area under the resulting H₂O trace.

Temperature preference experiment

We tested the preferred body temperature of 71 geckos (40 from the Mediterranean sites: 24 from Nahal Oren, 16 from Hurbat Burgin, and 31 from the desert sites: 16 from Nahal Ze'elim and 15 from Nahal Atadim; Table S3) by placing each individual on a 150×50 cm thermal gradient in which one side was heated to 50°C by a hot bath and the other end was cooled down to 18°C by a cold bath (Liwanag et al., 2018). Temperatures varied linearly across the thermal gradient. We then put animals individually in two separate tracks in parallel on the middle of the thermal gradient and recorded their body temperature every 10 s using a data logger (Besag K thermometer SD logger 88 598) connected to a thermocouple inserted and fixed with medical tape (Vetrap bandaging tape) in the cloaca for 21 h. By measuring individuals over 21 h, rather than for 2-5 h during the morning or noon as is common practice with diurnal and heliothermic species (Camacho & Rusch, 2017), we were better able to capture the thermal range of this species, which has a bimodal activity pattern (active during the early morning and evening; Schwarz et al., 2021). We did not use an open photothermal gradient, as is commonly used for measuring lizards (Camacho & Rusch, 2017 and citations therein), because P. guttatus has adhesive toepads which allow it to climb the glass walls of such terraria. Incandescent light bulbs warm up the glass walls of the terrarium, and geckos can inadvertently burn their feet. Additionally, climbing adds the dimension of height to the thermal gradient. Using a closed, short design, such as ours (Liwanag et al., 2018), ensures the thermal gradient is two-dimensional for climbing species, also preventing their escape. For each individual, we calculated the mean preferred temperature in the lab over the whole period recorded, omitting the measurements of the first hour, which may have been influenced by handling (20 h).

Morphological measurements

We measured the SVL (snout-vent length), and the humerus, fore crus, femur and hind crus lengths of each individual using a digital caliper (to 0.01 mm precision) and weighed them using Pesola spring scales to 0.2 g precision, upon capture. For each individual, we calculated the forelimb length by summing the lengths of the humerus and fore crus, and the length of the hind limb by summing the tibia and hind crus. The body condition measure we used for the geckos was the residuals of a regression of log₁₀-transformed mass as the response variable against the log₁₀-transformed SVL of each individual as the predictor (Schulte-Hostedde et al., 2005). We counted the number of mites on each individual upon capture as a measure of ectoparasite load (Er-Rguibi et al., 2021), by examining all parts of the geckos equally. We did not use a magnifying glass because mites are well visible to the naked eye.

Statistical analyses

All data pertaining to the experiments and measurements are summarized in the Table S2. To test the effect of biome on metabolic rate and evaporative water loss in cold (25°C) and warm (35°C) temperatures, we constructed mixed-effects models using the "lme" function from the "nlme" package (Pinheiro et al., 2020), testing each trait at both the locality and biome levels. We omitted geckos that had only reliable data for one temperature regime but not the other. In the model for resting metabolic rate, we used the O2 consumption rate in $mL \times min^{-1}$ as the response. The AIC for the model including the log₁₀-transformed O₂ consumption rate was higher (biome model: AIC = 110.4) than the model for the non-transformed response (biome model: AIC = -653.3); therefore, we used the non-transformed response for O2 consumption rate. In the model testing, the evaporative water loss we used the log10transformed evaporative H₂O loss rate in $\mu L \times h^{-1}$ as the response (Table S2), as the log_{10} -transformed model (biome model: AIC = 215.2) was better than the non-transformed model (biome model: AIC = 539.6). In all models, we included the temperature regime (25°C-"cold"/35°C-"hot"), body mass (non-transformed for O2 consumption rate and log₁₀-transformed for water loss rate models- to reduce heteroskedasticity), sex and the number of days between the day of capture and the day of undergoing the experiment as fixed variables. We included the biome (Mediterranean/desert) from which geckos were collected in one model, and the locality (Mediterranean: Nahal Oren, Burgin, Desert: Nahal Ze'elim and Nahal Atadim) in another, as further fixed variables, as well as the interactions between biome/locality and temperature regime, and between the temperature regime and mass. In both models, we included the number of mites on individuals and its interaction with biome/locality as fixed effects. In the biome level model, we included the identity of the individual geckos and the locality it was collected from as random factors to account for both the nested design and the fact that each individual went through the experiment twice, once in each temperature regime. In the model for the locality level, we included only the identity of the individual geckos as a random factor to account for the fact that each individual went through the experiment twice, once in each temperature regime.

To determine whether geckos from different biomes differed in their preferred temperatures we constructed a nested mixedeffects model including the mean preferred temperature [°C] of each individual in the lab over 20 h as the response, with the biome, sex, and mass, as fixed effects, and the locality as a random factor, to account for the fact that locality is nested in the biomes. To test whether the preferred body temperatures of geckos differed between the localities they were collected from, we used an ANCOVA test with the mean preferred body temperature as the response, and locality and sex as main effects, with the body mass as covariate. In both models, we included the number of days between the day of capture and the day of undergoing the experiment as a main effect. We collected individuals from different localities at different months (and one of the four populations was sampled a year later than the others). However, we found no effect of collection day (in Julian date) on the ecophysiological traits in preliminary analyses. Therefore, we did not include dates in following analyses. For each individual we also calculated the preferred temperature in the lab at the same time of day it was caught in the field. We did that by averaging the temperatures recorded in the lab for each individual for an hour around the time of day it was collected in the field- 30 mins before and 30 mins after that time. Due to a malfunction of the thermometer, we omitted 12 individuals from Nahal Ze'elim (desert), and one from Hurbat Burgin (Mediterranean), the body temperatures of which could not be measured in the field. To compare the body temperatures measured in the field with those preferred in the lab across biomes and localities, we constructed two mixed-effects models with the mean body temperature as the response variable. In the biome level model, we included the biome and the measurement location (lab/field), and their interaction, as fixed effects, and the identity of the individual nested in the locality as random effects, to account for the fact that each individual was measured twice (in the field and in the lab), and that the localities are nested in the biomes. In the locality level model, we included the locality and the measurement location (lab/field), and their interaction, as fixed effects, and included the identity of the individual nested in the locality as a random effect, to account for the fact that each individual was measured twice (in the field and in the lab).

To test whether geckos from the different biomes differed in body condition and limb sizes, we constructed three mixedeffects models, including the biome as fixed effect and the locality as a random effect, to account for the fact that localities are nested in the biomes. In the model testing body condition we included the log_{10} -transformed mass of each individual as the response variable and the SVL (log_{10} -transformed), sex, and number of mites, as fixed effects (Er-Rguibi et al., 2021; Hawlena et al., 2010). We also performed an ANOVA including the number of mites on each gecko as the response, and the locality it belongs to as the predictor, to determine if there are differences in mite load among localities. In the two models testing for limb lengths, we included the log_{10} - transformed forelimb or hind limb length of each individual as the response variable and the SVL (log_{10} -transformed) and sex (males are larger than females, Bar et al., 2021) as fixed effects. We then constructed three ANCOVA models, one for each trait, including the locality and sex as main effects.

In all analyses, we selected the best models via backward stepwise elimination based on *P*-values ($\alpha = 0.05$). To determine which relationship contrasts were significant in each model, we performed a "Tukey" HSD post hoc test, using the function "emmeans," implemented in the R package "emmeans" (Lenth, 2020). All statistical analyses were performed with R v3.6.2 (R Core Team, 2019). The statistical analysis' R script is provided in full in the Appendix S1.

Results

We successfully obtained data on temperature preferences in the lab of 68 individuals, metabolic rates of 56 individuals, and evaporative water loss rates of 55 individuals, from the four localities (Table 1). We were not able to obtain a full set (in both temperature regimes) of metabolic rate and evaporative water loss data for 12 and 13 collected individuals, respectively, because we discarded trials in which geckos moved or defecated. We obtained field body temperatures of 55 individuals, SVL, and forelimb measurements of 71 individuals, and hind limb measurements of 70 individuals (Table 1).

Resting metabolic rate

There was no significant difference between the VO₂ of geckos from the different biomes (full model: t = -0.28, P = 0.81; Fig. 2a), or localities (Table S3; Fig. 2b), in either temperature regime (t = 1.37, P = 0.18; Table S3). There was also no difference between the resting metabolic rates of females and males (t = 0.72, P = 0.48), no effect of the number of days in captivity (t = 1.39, P = 0.17), and no interaction between the biome and temperature regime (t = 0.31, P = 0.76), or locality and the temperature regime (Table S3). In the best model, VO₂ increased with increasing body mass at a faster rate in the high-temperature regime (best model: slope = $3.7 \times 10^{-3} \pm 3.5 \times 10^{-4}$, intercept = $-2.1 \times 10^{-3} \pm 3.0 \times 10^{-3}$ mL × min⁻¹, t = 10.65, P < 0.0001) than in the low (slope = $2.2 \times 10^{-3} \pm 3.5 \times 10^{-4}$, t = 6.18, P < 0.0001) temperature regime (interaction term: t = 3.61, P = 0.0007; Fig. 2c).

Evaporative water loss

There was no significant difference between the evaporative water loss rates of geckos from the two biomes (full model: t = -0.96, P = 0.44; Fig. 2d; Table S4a) in either temperature regime (t = -0.79, P = 0.43; Table S4b). There was also no difference between females and males (t = 1.96, P = 0.06), no effect of the number of days in captivity (t = 0.66, P = 0.52), or the number of mites (t = -1.074, P = 0.29) and no interaction between temperature regime and biome (t = 1.91, P = 0.06), mass and temperature regime (t = -0.63, P = 0.54) or between biome and mite load (t = 0.40, P = 0.69, n = 55). After model selection, the evaporative water loss rate of geckos



Figure 2 Boxplots of the residuals of the regression between \log_{10} -transformed resting metabolic rate [mL x min⁻¹] against body mass [g] in the low (25°C; blue triangles and dashed line) and high (35°C; red circles and solid line) temperature regimes tested in the laboratory, of geckos from (a) the Mediterranean and the desert, and (b) the four localities, (c) and the regression between the O₂ consumption rate [mL x min⁻¹] and body mass [g] of all geckos in the two temperature regimes tested in the laboratory. Boxplots of the residuals of the regression between \log_{10^-} transformed evaporative water loss rate [μ L x h⁻¹] against body mass [g] in the low (blue) and high (red) temperature regimes tested in the laboratory, of geckos from (d) the Mediterranean and the desert biomes, and (e) the four localities, and the (f) regression between the evaporative H₂O loss rate [μ L x h⁻¹] and body mass [[g]; both log₁₀-transformed) of all geckos in the two temperature regimes tested in the laboratory (low: 25°C; blue triangles and dashed line; high: 35°C; red circles and solid line). The Nahal Ze'elim and Nahal Atadim are in the desert biome, Hurbat Burgin, and Nahal Oren are in the Mediterranean biome.

increased with increasing body mass (best model: slope = 1.03 ± 0.19 , intercept = -0.21 ± 0.40 , t = 5.57, P < 0.0001) and was higher by 81% in the high-temperature regime (best model: mean = $0.62 \ \mu L \times h^{-1}$) compared with the low one (mean = 0.07 μ L × h⁻¹, t = 9.72, P < 0.0001; Fig. 2f). At the locality level, there was a small positive effect of the number of days in captivity on the water loss of geckos (best model: intercept = $0.069 \pm 0.46 \ \mu L \times h^{-1}$, slope = $4.9 \times 10^{-3} \pm 2.0 \times 10^{-3} t = 2.43$, P = 0.02), and males lost 22% more water than females (t = 2.44, P = 0.02). While in all localities geckos lost more water in the hightemperature regime than in the low one, geckos from Nahal Oren (Mediterranean) lost the same amount of water in both temperature regimes (t = 0.17, P = 0.86; Fig. 2e; Table S4c). Additionally, geckos from Nahal Oren lost less water in the high-temperature regime than geckos from Hurbat Burgin (t = 3.06, P = 0.02; Mediterranean) but more than geckos from Nahal Ze'elim (t = -2.87, P = 0.03; desert; Fig. 2e; Table S4d). There were significantly more mites on individuals from Nahal Atadim (mean = 8 ± 2 , t = 3.55, P = 0.003; desert), Nahal Oren (mean = 9 ± 1 , t = 4.48, P = 0.0001), and Hurbat Burgin (mean = 6 ± 1 , t = 2.70, P = 0.04)

compared with individuals from Nahal Ze'elim (mean = 0.06 ± 0.06), but the number of mites on individuals was not associated with the water loss rates of geckos across localities (t = -1.24, P = 0.22).

Temperature preference

The mean preferred temperature of geckos from the desert (mean = 33.1 ± 0.9 °C) was not statistically significantly different than the mean preferred temperature of Mediterranean geckos (full model: mean = 32.0 ± 0.9 °C, t = 1.59, P = 0.25; Fig. 3a). Body mass was not correlated with temperature preference (full model: slope = 0.02 ± 0.07 , t = 0.27, P = 0.79), there was no difference between and males (mean = $32.9 \pm 0.9^{\circ}$ C) and females (mean = $32.0 \pm 0.9^{\circ}$ C, t = 0.40, P = 0.69), and no effect of the number of days in captivity (t = 1.99, P = 0.05). When analyzing the locality level however, there was a small positive effect of the number of days in captivity on the temperature prefered (best model: slope = $0.01 \pm 5.9 \times 10^{-3}$, t = 2.22, P = 0.03, n = 68). Additionally, the mean preferred temperature of geckos from Nahal Atadim (mean = 33.7 ± 0.4 °C; desert) was significantly

Ecophysiological variation in desert versus Mediterranean gecko populations



Figure 3 Boxplots of the mean body temperature measured in three origins: in the lab-calculated over 20 h of measurement, in the labcalculated over 1 h around capture time, and in the field upon capture, between (a) the Mediterranean (turquoise) and the desert (orange) biomes, and (b) the four localities (orange = Nahal Ze'elim; yellow = Nahal Atadim; green = Hurbat Burgin; blue = Nahal Oren). The Nahal Atadim and Nahal Ze'elim localities are in the desert biome, and Nahal Oren and Hurbat Burgin are in the Mediterranean biome. The diamonds represent the means.

higher than the mean preferred temperature of geckos from Hurbat Burgin (mean = $32.2 \pm 0.5^{\circ}$ C, t = -2.72, P = 0.03; Mediterranean), and Nahal Oren (mean = $31.7 \pm 0.4^{\circ}$ C, t = 4.15, P = 0.0006; Mediterranean), but similar to that of geckos from Nahal Ze'elim (mean = $32.3 \pm 0.6^{\circ}$ C, t = 2.36, P = 0.1; Fig. 3b; desert). Geckos from Nahal Oren had a similar mean preferred temperature as geckos from Nahal Ze'elim (t = -1.34, P = 0.54), and Hurbat Burgin (t = 1.17, P = 0.65; Fig. 4b), and those from Hurbat Burgin had similar preferred temperatures as geckos from Nahal Ze'elim (t = -0.22, P = 1.0).

Field body temperatures

The body temperatures measured in the field upon capture were 3 and 7.5°C lower than those preferred in the lab, at the same time of day, for geckos from the desert (mean in field = 31.0 ± 1.8 °C, mean in lab = 34.0 ± 1.8 °C, t = -3.02, P = 0.004),and the Mediterranean (mean in field = 24.6 \pm 1.8°C, mean in lab = 32.1 \pm 1.8°C, n = 56, t = 8.28, P < 0.0001) biomes, respectively (Fig. 3a). The body temperatures of Mediterranean and desert geckos, however, were similar in the field (t = 2.51, P = 0.13) and in the lab (n = 56, t = 0.75, P = 0.53; Fig. 3a). Within localities, field body temperatures were lower by 4, 5, and 11°C than those preferred in the

lab for geckos from Hurbat Burgin (Mediterranean). Nahal Atadim (desert), and Nahal Oren (Mediterranean), respectively, but not in those from Nahal Ze'elim (Fig. 3b; Table S5a; desert). While the mean temperatures preferred in the lab over 20 h were similar across localities (Fig. 3b; Table S5b), field body temperatures of geckos from Nahal Oren (mean = $21.0 \pm 0.8^{\circ}$ C, n = 16) were lower than those of geckos from Nahal Atadim (mean = 28.6 \pm 0.8°C, n = 15, t = -6.65, P < 0.0001), Hurbat Burgin (mean = 28.4 ± 0.8 °C, n = 15, t = -6.51, P < 0.0001), and Nahal Ze'elim (mean = 34.2 ± 1.1°C, n = 9, t = -10.04, P < 0.0001; Fig. 3b; Table S5b). The field body temperature of geckos from Nahal Ze'elim was also significantly higher than that of geckos from both Hurbat Burgin (t = 4.38, P = 0.0003), and Nahal Atadim (t = 4.26, P = 0.0005; Fig. 3b; Table S5b). The field body temperatures of geckos from Nahal Atadim were similar to that of geckos from Hurbat Burgin (t = 0.14, P = 1.0; Fig. 3b; Table S5b).

Morphological characteristics

The body condition of geckos did not differ between sexes (t = 1.10, P = 0.27; Fig. 4a), or biomes (t = 0.24, P = 0.83; Fig. 4b), and was not affected by the number of mites found on individuals (t = 1.10, P = 0.27). When analyzing the locality level, however, the body condition of geckos from Nahal



Figure 4 Boxplots of morphological traits: (a–c) body condition as mass against SVL (residuals, both \log_{10} -transformed), (d–f) forelimb length corrected for SVL and (g–i) hind limb length between (a, d, g) males (purple) and females (light green), between geckos from (b, e, h) the Mediterranean (turquoise) and the desert (orange) biomes and (c, f, i) the four localities (orange = Nahal Ze'elim; yellow = Nahal Atadim; green = Hurbat Burgin; blue = Nahal Oren). The values in the y-axis are residuals of the regression between fore limb or hind limb lengths and the SVL (d–i), all \log_{10} -transformed. The Nahal Atadim and Nahal Ze'elim localities are in the desert biome, and Nahal Oren and Hurbat Burgin are in the Mediterranean biome.

Oren (Mediterranean) was higher by $\sim 2\%$ than that of geckos from Nahal Ze'elim (t = 3.21, P = 0.01; desert) and Hurbat Burgin (t = 3.37, P = 0.007; Mediterranean), but similar to that of geckos from Nahal Atadim (t = 1.27, P = 0.58; Fig. 4c; Table S6a; desert).

The forelimb lengths of geckos increased by 0.69% for every 1% increase in SVL (best model: intercept = 0.12 ± 0.13 mm, slope = 0.69 ± 0.07 , n = 71, t = 9.81, P < 0.0001). There was no significant difference between the forelimbs of males (Full model: mean = 25.3 ± 0.3 mm) and females (mean = 23.8 ± 0.3 mm, t = 1.10, P = 0.28; Fig. 4d), and no difference between biomes (t = 2.50, P = 0.13; Fig. 4e). At the locality level the SVL-corrected forelimbs of geckos from Nahal Atadim (desert), and Nahal Ze'elim (desert), were longer on average than those of geckos from Nahal Oren (Mediterranean) by 30% and 28%, respectively (Fig. 4f; Table S6b). There was no difference, however, between the forelimb lengths of geckos from Nahal Atadim and those from Hurbat Burgin (Mediterranean), or Nahal Ze'elim, and between the forelimb lengths of geckos from Hurbat Burgin and those from either Nahal Oren or Nahal Ze'elim (Fig. 4f; Table S6b). The hind limbs of geckos increased by 0.54% for every 1% increase in SVL (best model: intercept = 0.48 ± 0.14 mm, slope = 0.54 ± 0.08 , n = 70,

t = 7.13, P < 0.0001). The hind limbs of males (mean = 31.3 ± 0.4 mm) were longer than those of females (mean = 29.4 ± 0.3 mm, t = 2.34, P = 0.02; Fig. 4g). The SVL-corrected hind limb lengths of geckos were similar across biomes (full model: t = -0.95, P = 0.44; Fig. 4h) and localities (Fig. 4i; Table S6c).

Discussion

We obtained mixed support for the hypothesis that geckos are adapted to the climate prevailing in their habitat. While none of the ecophysiological traits we tested differed between individuals from the desert and Mediterranean biomes, the evaporative water loss rates, temperature preferences, body conditions and forelimb lengths differed between some of the localities, but not always in the direction we predicted.

We tested geckos from two biomes in two temperature regimes in the laboratory, and geckos from all biomes and localities had similar metabolic rates in the high $(35^{\circ}C)$ and the low $(25^{\circ}C)$ temperature regimes. This implies that in this study system, the metabolic rates of *P. guttatus* populations seem to respond to temperature similarly. This supports the "universal thermal dependence" hypothesis which claims that

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the sensitivity of metabolic rate to temperature (i.e., the rate of metabolic rate increasing with temperature) varies little across taxa (Brown et al., 2004). Our results, therefore, support the claim that resting metabolic rate is a conserved trait and suggest that the variation in metabolic rates, and consequently natural selection and adaptation to local conditions, are limited (Réveillon et al., 2019). Low dependence of metabolic rate on the ambient temperature may be the result of great thermal plasticity in this species, allowing it to prevail in two biomes across its range. On the other hand, the resting metabolic ratebody mass relationship (Fig. 2c) of geckos across localities and biomes was steeper in the high-temperature regime. Thus, the resting metabolic rates of large individuals were almost twice higher in the high-temperature regime (35°C) compared with the lower one (25°C), while smaller individuals performed similarly in both temperature regimes in the lab. Therefore, the effect of temperature manifests only in large-bodied geckos. This discrepancy implies that the metabolic rate of larger individuals may be more influenced by the ambient temperature than that of small individuals. This suggests that large individuals may be more prone to deleterious effects caused by high metabolic rates, such as oxidative stress (Sohal & Allen, 1986). As temperatures increase with global warming, a small body size may be preferable and selected for, as has been previously found for both endotherms and ectotherms (Daufresne et al., 2009; Dubiner & Meiri, 2022; Genner et al., 2010; Gardner et al., 2011; Peralta-Maraver & Rezende, 2021; Sheridan & Bickford, 2011).

We found no statistically meaningful differences in the water loss rates of desert and Mediterranean geckos in the hightemperature regime, contradicting our hypothesis. When tested across localities, some differences were evident, but not in the way we predicted. The fact that all geckos, except those from Nahal Oren (Mediterranean), lost more water when tested in the high-temperature regime implies that they all respond to temperature in a similar way, and suggests that there is no adaptation to the different localities' microclimates. Our results stand in contrast to previous research on other lizard species and populations, in which lizards from colder microclimates lost more water than those from hot microclimates (Araya-Donoso et al., 2022; Belasen et al., 2017; Cox & Cox, 2015; Duvdevani & Borut, 1974; Hlubeň et al., 2021; Mautz, 1982; Sannolo et al., 2020). The fact that geckos from Nahal Oren lost water at similar rates in both temperature regimes, and did not lose water at the highest rate among populations is surprising, given the fact that this population is from the northernmost wettest locality we sampled (Table S1). Perhaps, this discrepancy resulted from Nahal Oren individuals being the most mite-infested of the four localities, consequently decreasing cutaneous water loss rates, a pattern that has been previously found in heavily infested populations from colder climates (Sannolo et al., 2020). Nevertheless, mite load on its own does not seem to be the main driver of water loss rates in our study system, because it was not directly related to water loss rates. Alternatively, Nahal Oren individuals might not have experienced the expected rates of water loss because they had the longest habituation period to laboratory conditions (Table S2). Further data on the water loss rates and parasite

infestation (by both mites and ticks) of additional populations of *P. guttatus* across its range are needed to elucidate this question.

Neither the preferred body temperatures of geckos, nor their body temperatures measured in the field, differed between the two biomes, contrary to our predictions. When compared between localities, however, some differences between localities were statistically significant, but do not support the "metabolic cold adaptation" hypothesis. Geckos from the northernmost Mediterranean locality (Nahal Oren) preferred lower body temperatures than those from the southernmost desert locality (Nahal Atadim; desert), against our prediction. This suggests that the northernmost population of Nahal Oren has adapted to its colder microhabitat by reducing its preferred (and potentially optimal) temperature, and possibly shifting its performance curve to lower temperatures, and not by increasing its preferred temperature and thereby its metabolic rate (Bodensteiner et al., 2021). The fact that there was a difference only between localities, but not between biomes, highlights the importance of the resolution at which temperature preference is tested.

Geckos in both biomes preferred higher body temperatures in the laboratory experiment than the body temperature they had when caught in the field. A similar pattern of lower body temperatures measured in the field compared with the lab is present in three localities, two from the Mediterranean biome (Nahal Oren and Hurbat Burgin) and one from the desert biome (Nahal Atadim). This can either mean that, during the time geckos were caught in the field, they did not reach their preferred temperature, or that they do not reach their preferred temperatures in either biome. Since the mean selected temperature in the lab was calculated for 1 h around the time of collection in the field was similar to the mean preferred temperature calculated over 20 h, we think that the possibility that our results are the product of collection time or month are improbable. Instead, if geckos do not reach their preferred body temperature in the field in either biome, even if they do at the hottest month of the year (August), it may suggest that despite their difference in preferred body temperatures, they have not adapted their thermoregulatory behaviors to maximize their performance in these habitats, as was found in other lizard species (Alés et al., 2017; Ibargüengoytía et al., 2010). The exception is the Nahal Ze'elim population from the desert biome, which showed no difference between the field and lab body temperatures and had higher field body temperatures compared with all other localities. This exception probably arises from the fact that Nahal Ze'elim, in the Judean Desert, is the hottest locality we measured, with air temperatures sometimes exceeding 40°C even at night in the summer (Table S1). The fact that this population had similar body temperatures measured in the field and in the lab, as opposed to the other populations that we studied, suggests that geckos from Nahal Ze'elim are the only ones that reach their preferred temperatures in the field. They may thus perform better than other populations as a consequence. P. guttatus belongs to a Saharo-Arabian genus, and thus the microclimate in Nahal Ze'elim may resemble more the microclimate in which this species has evolved, than that which prevails in localities at the northernmost edge of its distribution. However, more information on how temperature preference is related to geckos' performance, and on the thermoregulation efficiency, and the thermal quality of the habitat across localities, is needed to gain a better understanding of what appears as a lack of adaptation to the microclimate in this species. Moreover, more data on additional populations from further localities in both biomes are essential for elucidating the extent of the difference between populations from the two biomes.

The body condition of geckos was similar across biomes and sexes, but not across localities. Body condition was unrelated to ectoparasite infestation. Previous studies found that larger individuals, which are often older, were more heavily infested by ectoparasites than smaller or younger individuals (Er-Rguibi et al., 2021), because they were exposed to parasite infection longer (Madsen & Ujvari, 2006). Others suggest that individuals with better body condition may tolerate higher levels of mite loads (Comas, 2019). This can also explain our results, as body condition is correlated with body size, and thus the populations with the largest individuals (Nahal Oren and Nahal Atadim; Table 1) were also the most infested. The factors influencing body condition of P. guttatus are not clear at this point, and studies evaluating more direct measures of primary productivity or food availability and analyzing the effects of various endoparasites are needed to gain a clearer picture.

The forelimbs of geckos from localities in the desert biome were longer than those of individuals from localities in the Mediterranean, as predicted by Allen's rule, but hind limb lengths were similar. Legs of beetles and ants have been found to be longer in populations occupying hotter environments than in colder habitats counterparts (Broza et al., 1983; De los Santos et al., 2000; Medvedev, 1965; Sommer & Wehner, 2012). Longer legs enable these insects to carry their bodies further away from the hot surface in desert habitats (Sommer & Wehner, 2012). Whether this hypothesis is the reason behind longer limbs in lizards from hot environments is, however, unknown, and more research is needed to test it.

Interestingly, some inter-population differences emerge only between localities within biomes, which suggests that the resolution of the comparison matters, even if it is only because of statistical power. Schwarz et al. (2021) studied ecophysiological trait differences between two populations of P. guttatus from opposing slopes of a canyon in Nahal Oren (Mediterranean) and found no differences in ecophysiological traits such as metabolic rate and water loss rate. Schwarz et al. (2021) suggested that much stronger contrasts in microclimatic conditions and physical distance are needed in order to drive trait differences. Based on our current study, this notion seems to be at least partially correct, as we did find differences in some traits between geckos from the most extreme localities in terms of distance and conditions: the northernmost (Nahal Oren; Mediterranean) and southernmost (Nahal Atadim; desert) localities (184 km), and between the most cold and mesic (Nahal Oren) and the most hot and arid (Nahal Ze'elim; desert) localities. A similar recent study tested the metabolic rate, temperature preference, and morphology of Liolaemus fuscus lizards along a \sim 600 km aridity gradient in Chile, with a mean annual precipitation of 492 mm versus 45 mm (Araya-Donoso

et al., 2022). They found lower evaporative water loss in desert compared with Mediterranean populations, but no differences in metabolic rates or temperature preferences (Araya-Donoso et al., 2022). In our study, however, along a narrower geographic cline of only 184 km, but a steeper, 20-fold versus 11-fold difference in precipitation (500 mm versus 25 mm mean annual precipitation; Table S2), geckos from the northernmost Mediterranean locality lost less water and preferred lower temperatures, but had similar metabolic rates, as geckos from the southernmost desert locality. This shows that interspecific differences in ecophysiological traits can manifest at less than a third of the distance existing between tested localities, depending on the species tested, its evolutionary history, and the geography and climate of its habitat. Nevertheless, it is important to note that our hypotheses were based on broadscale climatic differences that may not be entirely relevant to the microclimates experienced by organisms at their specific microhabitat. Thus, a modeling approach that can consider both the microclimates experienced by each individual and climatic variables at a broader scale might shed more light on the physiological differences and adaptation of this species to its habitat.

To conclude, our results suggest that some ecophysiological traits may be more evolutionary conserved among populations and even across species, and some may be more dependent on the microclimate in the habitat. The ecophysiological traits we studied are potentially plastic. If so, this plasticity may have contributed to the species range. Furthermore, this plasticity may benefit this species' ability to prevail in its environment under a global warming scenario.

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Author contributions

RS, SM, and DC conceived the ideas and designed methodology; RS, EL, and GS collected the data; RS analyzed the data; RS and SM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Permits and ethics

The study has been conducted under permits no. 2018/42082, 2019/42284 and 2020/42554 from the Israeli Nature and Parks Authority, and under permit no. 04-19-077 from the Tel Aviv University ethics in animal experimentation committee.

Conflict of interest

The authors herby state that there is no conflict of interest.

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Data availability

The data supporting this article are available in the article and in its online supplementary material.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Statistical analysis code in R.

Table S1. Temperatures, humidity, and precipitation means for the four collection localities.

Table S2. Full data table.

 Table S3. Models for metabolic rate between biomes and localities in two temperature regimes.

Table S4. Post hoc results for the comparison of evaporative water loss between biomes and localities in two temperature regimes.

 Table S5. Post hoc results for the comparison of field and lab temperatures between biomes and localities.

Table S6. Post hoc results for the comparison of body condition and limb lengths between biomes and localities.