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# A global analysis of field body temperatures of active squamates in relation to climate and behaviour

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## Abstract

**Aim:** Squamate fitness is affected by body temperature, which in turn is influenced by environmental temperatures and, in many species, by exposure to solar radiation. The biophysical drivers of body temperature have been widely studied, but we lack an integrative synthesis of actual body temperatures experienced in the field, and their relationships to environmental temperatures, across phylogeny, behaviour and climate.

**Location:** Global (25 countries on six continents).

**Taxa:** Squamates (210 species, representing 25 families).

**Methods:** We measured the body temperatures of 20,231 individuals of squamates in the field while they were active. We examined how body temperatures vary with

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substrate and air temperatures across taxa, climates and behaviours (basking and diel activity).

**Results:** Heliothermic lizards had the highest body temperatures. Their body temperatures were the most weakly correlated with substrate and air temperatures. Body temperatures of non-heliothermic diurnal lizards were similar to heliotherms in relation to air temperature, but similar to nocturnal species in relation to substrate temperatures. The correlation of body temperature with air and substrate temperatures was stronger in diurnal snakes and non-heliothermic lizards than in heliotherms. Body-substrate and body-air temperature correlations varied with mean annual temperatures in all diurnal squamates, especially in heliotherms. Thermal relations vary with behaviour (heliothermy, nocturnality) in cold climates but converge towards the same relation in warm climates. Non-heliotherms and nocturnal species body temperatures are better explained by substrate temperature than by air temperature. Body temperature distributions become left-skewed in warmer-bodied species, especially in colder climates.

**Main Conclusions:** Squamate body temperatures, their frequency distributions and their relation to environmental temperature, are globally influenced by behavioural and climatic factors. For all temperatures and climates, heliothermic species' body temperatures are consistently higher and more stable than in other species, but in regions with warmer climate these differences become less pronounced. A comparable variation was found in non-heliotherms, but in not nocturnal species whose body temperatures were similar to air and substrate irrespective of the macroclimatic context.

#### KEYWORDS

air temperature, body temperature distribution, climate, heliotherm, lizard, nocturnal, reptile, snake, substrate temperature, thermal ecology

## 1 | INTRODUCTION

Body temperatures of reptiles and other ectotherms are dependent on the environment. An individual's body temperature influences its metabolism (Andrews & Pough, 1985; Sears, 2005; Theisinger et al., 2017), life history (Cadby et al., 2014; Meiri et al., 2013), behaviour (Gunderson & Leal, 2015; Henle, 1992; Ord & Stamps, 2017) and ecology (Niewiarowski & Waldschmidt, 1992; Pafilis et al., 2007; Van Damme et al., 1989, 1991). Consequently, body temperature plays a critical role in shaping ectotherm fitness (Angilletta, 2009; Angilletta et al., 2002; Cadby et al., 2014). Although reptiles cannot efficiently harness metabolic heat to maintain a constant physiologically optimal body temperature, this does not mean that they are at equilibrium with the temperature of their surroundings. Many species have strategies to keep their body temperature within suitable limits (Bauwens et al., 1990; Cowles & Bogert, 1944; Huey, 1982; Porter & Tracy, 1983; Valdecantos et al., 2013) by behaviourally regulating their exposure to heat sources, thereby buffering the detrimental effects of environmental thermal variation (Kearney et al., 2009; Muñoz & Losos, 2018). The factors determining heat exchange between the body and its environment are well-understood

(Kearney et al., 2013). They include factors such as air and substrate temperature (Muth, 1977; Porter & Tracy, 1983) as well as body size and posture (Muth, 1977; Stevenson, 1985), among others (e.g. wind speed, evaporative cooling, body colour). Solar radiation provides an additive source of heat beyond the equilibrium of heat exchange with the surroundings (Bakken et al., 1985; Pianka & Huey, 1978; Shine & Kearney, 2001), and many species take advantage of this, basking in the sun to maintain their body temperatures high and within a narrow range (Cowles & Bogert, 1944; Dreisig, 1984), presumably near their thermal optima. While individuals may seek or avoid direct sunlight under different conditions (e.g. during the day, season and with reproductive status; Huey & Pianka, 1977; Huey et al., 2003; Otero et al., 2015; Vicenzi et al., 2019), species can be broadly categorized by behaviour into those that often bask in the sun ('heliotherms'), and those that do not. The latter can be further divided by their activity cycle, into diurnal and nocturnal taxa.

Studies on squamate body temperatures in relation to environmental temperatures are numerous. Some tested thermal traits under laboratory conditions, such as preferred temperature and critical temperature limits (e.g. Diele-Viegas et al., 2018; Grigg & Buckley, 2013; Labra et al., 2009). Many researchers gather field

measurements of active squamates in their natural habitats. These field studies are mostly localized and focus on one or a few species, but a few large-scale data sets were compiled (Brattstrom, 1965; Meiri et al., 2013; Pianka et al., 2017), and several studies attempted to synthesize body temperatures across many species in relation to habitat characteristics or species traits. These studies describe patterns such as a diurnal–nocturnal divide in body temperature (Huey & Slatkin, 1976; Moreira et al., 2021), higher body temperatures in thermoregulating taxa (Diele-Viegas et al., 2018), climatic influences on body temperature (Giacometti et al., 2023; Meiri et al., 2013) and evolutionary patterns in body temperature (Ibargüengoytia et al., 2021; Labra et al., 2009; Moreno Azocar et al., 2013). These and similar meta-analyses only examined mean values for each species, which does not allow for detecting patterns in the underlying distributions and variability (Hertz et al., 1993). This loss of information can be ameliorated by using the full data on individual temperature measurements, taking thermal distributions into account and enabling examination of each species' variation along the range of environmental temperature variables in its habitat (Henle, 1992).

One aspect of this variation can be seen in the regression between body temperature ( $T_b$ ) and substrate or air temperature ( $T_{sub}$  or  $T_a$ , respectively). This method was widely used in the past as a limited measure of thermoregulation (Bauwens et al., 1990; Huey & Pianka, 1977; Huey & Slatkin, 1976) prior to the common implementation of methods for measuring operative temperatures (Hertz et al., 1993). The regression approach, however, is still useful in providing an ecological context to measurements of body temperature (Pianka et al., 2017; Pianka & Vitt, 2003), often used together with operative temperature models (e.g. Kapsalas et al., 2018; Labra et al., 2009; Ortega et al., 2016; Rock et al., 2002; Valdecantos et al., 2013). High intercepts and shallow slopes for the relationship between  $T_b$  and environmental temperature indices (e.g.  $T_{sub}$  or  $T_a$ ) are often taken to indicate that the animals maintain a high and stable body temperature across a wide range of environmental temperatures (e.g. Bauwens et al., 1990; Huey & Pianka, 1977; Ortega et al., 2016; Valdecantos et al., 2013), whereas intercepts approaching zero with slopes approaching one imply that  $T_b$  is fully coupled with, thus closely matches, the environmental variation (e.g. Kapsalas et al., 2018; Rock et al., 2002; Ruibal & Philibosian, 1970; but see Heath, 1964). Pianka and Vitt (2003) and Pianka et al. (2017) further suggested that the slopes and intercepts of these regressions are measures of microhabitat and activity which can be used to represent a lizard's ecology.

Beyond the statistical relationship between body and environmental temperatures, examining the full temperature data, rather than just the means, can provide insights into the frequency distribution of a species' body temperatures. Huey and Pianka (2018) found that body temperature distributions of diurnal desert lizards were left-skewed, with a mode near the warmer end of the  $T_b$  range with a long 'tail' across a wide range of lower temperatures. Left-skewed body temperature distributions are deemed better for squamate activity due to the similar asymmetry of performance curves, such that exceeding the optimum temperature leads to a sharper

drop in performance or fitness than a shift of a similar magnitude towards lower temperatures (Martin & Huey, 2008). This, however, is probably only true for squamates active at high temperatures, where the optimum is nearer the maximum, such as the diurnal lizards studied by Huey and Pianka (2018), and has not been studied in other groups.

Differences in thermal ecology among species can be driven by macroclimatic conditions (Rubalcaba et al., 2023). For example, lizards in colder regions thermoregulate more often, to make the most of the low heat availability and the short season suitable for activity (Anderson et al., 2022; Caldwell et al., 2017; Gómez Alés et al., 2017; Gvoždík, 2002). Tropical squamates, on the other hand, may allocate less time and resources to thermoregulation (Shine & Madsen, 1996), since the thermal quality of the habitat is high throughout the day and year, not requiring exploitation of rare thermal opportunities (Blouin-Demers & Nadeau, 2005). A large-scale study by Meiri et al. (2013) found almost no correlation between mean body temperature and mean annual air temperature of a species' distribution. They suggested that in cold regions, lizard activity is restricted to the hottest hours of the day and only the warmest times of the year, masking the effects of the generally low temperatures.

To date, however, multi-species studies are still mostly restricted to a few regions or biomes, and overwhelmingly focus on lizards—especially diurnal, basking lizards. Therefore, despite these syntheses and the ample body of literature on individual species, we still lack a large-scale comparative analysis across taxa and regions. We aimed to gain a global perspective of how squamate body temperatures in the field relate to the temperature of their immediate surroundings, under the influence of different macroclimatic contexts and behavioural factors.

## 2 | METHODS

### 2.1 | Field measurements

We (all authors of this work) caught active squamates in the field, in many sites across the world (Figure 1), and measured their body temperatures ( $T_b$ ). We then measured substrate temperatures ( $T_{sub}$ ) and/or air temperatures ( $T_a$ ) at the specific location where each individual was found. The method of measurement varied among groups. Most of us took cloacal temperatures using either a digital thermocouple or an analogue thermometer, but in a few cases body temperature was measured using an infrared thermometer (measuring skin temperature) or temperature-sensitive radio transmitters (see Table S1). Cloacal temperatures were taken immediately (no more than 1 min) after the individual was caught. Note that these environmental temperature data are used here in the absence of measurements of other thermal properties of the environment. Thus, they do not enable to qualify thermal quality and thermoregulatory strategy and efficiency (Hertz et al., 1993). Protocols were consistent for each species, and therefore could be corrected for in the statistical models (see Section 2.3).

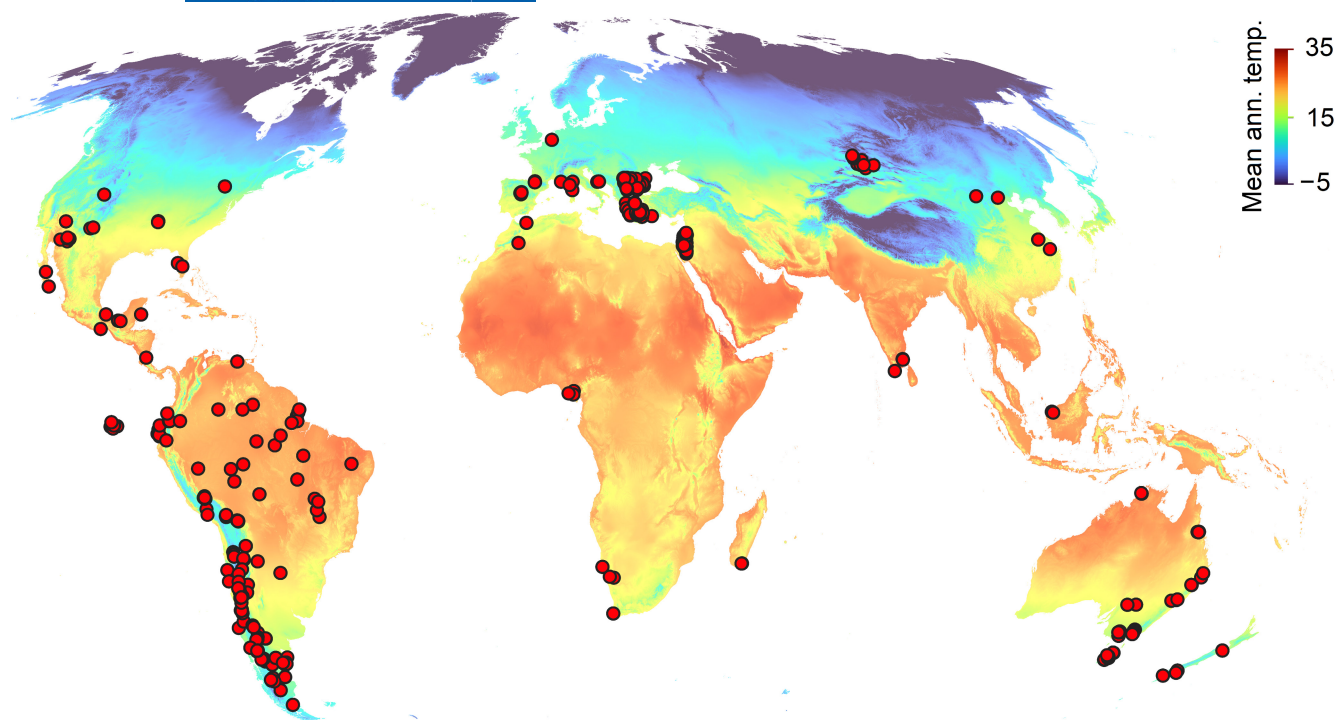


FIGURE 1 Locations of all the body temperature data in our data set (25 countries). The map is in Mollweide equal-area projection and coloured by mean annual temperatures.

## 2.2 | Species trait categorization

We filtered the data to include only species with records from at least 20 individuals per species. To account for phylogenetic non-independence in the subsequent statistical analyses, we used the full imputed phylogenetic tree of Tonini et al. (2016). Species absent from this phylogenetic tree were inserted into it manually when possible (in place of a sister species or into an existing polytomy) and otherwise were excluded from the analysis. Since the Tonini et al. tree contains several polytomies, which are known to affect phylogenetic analyses (Molina-Venegas & Rodríguez, 2017), we repeated all of the analyses using the tree from Zheng and Wiens (2016) which has 42 fewer species but is fully resolved.

We divided species by diel activity and basking behaviour, according to the literature and our own observations. We did not base the partitioning of species on the temperature measurements to prevent circularity of the definitions (Vitt et al., 1998). We classified species according to these behavioural categories, rather than between thermoregulators versus thermoconformers, because the latter is unknown for many species, and because discerning between thermoconformers and actively regulating thigmotherms is difficult (Doan et al., 2022; Hertz et al., 1993). We categorized species that are not commonly observed exhibiting basking behaviour as 'non-heliothermic' rather than 'thigmotherms', since we classified them by observable behaviour and not according to the sources of heat gain and loss, of which we cannot be sure without direct testing. That is, each researcher or group classified the behaviour of the species which they contributed to the database, according to the literature

and their own observations and expertise. This classification, while qualitative and to an extent subjective, was carried out before any of the analyses to prevent them from being biased by the authors' hypotheses. Diurnal snakes were placed in a separate category despite basking, since their thermal biology is considered distinct from that of the more commonly studied lizards (Avery, 1982; Gibson & Falls, 1979; Whitaker & Shine, 2002). We did not have measurements of enough nocturnal snake species to include them as a separate category and grouped them with the nocturnal lizards. Species were classified into four categories: (1) 'heliotherms' (heliothermic lizards), (2) 'non-heliotherms' (diurnal non-heliothermic lizards), (3) 'diurnal snakes' and (4) 'nocturnal species'. We derived the mean annual temperature, as a proxy for the macroclimatic conditions, at the site where each species was measured (1970–2000 average, data from BIO1 in WorldClim; Fick & Hijmans, 2017). When we had no body mass data for a species from measurements of the individuals used in the temperature measurements, we estimated it from mean species snout-vent length data (either from the individuals measured or from Meiri et al., 2021) using allometric equations from Feldman et al. (2016) and Meiri et al. (2021).

## 2.3 | Statistical analysis

For each of the species, we calculated mean  $T_b$ , mean  $T_{sub}$ , mean  $T_a$  and  $T_b$  skewness (using the 'moments' package in R; Komsta & Novomestky, 2015). For each of the species (pooling all sites together), we performed linear regressions of  $T_b$  against  $T_{sub}$  and



(separately)  $T_a$ , to obtain species-specific intercepts, slopes and  $R^2$  values. We further regressed  $T_b$  as a response variable with both  $T_{sub}$  and  $T_a$  as predictors for the individuals for which we had both  $T_{sub}$  and  $T_a$  measurements. We then obtained partial  $R^2$  values for  $T_{sub}$  and  $T_a$ . Because body temperature is often strongly influenced by evolutionary relatedness (Bogert, 1949; Grigg & Buckley, 2013; Huey & Pianka, 1977; Huey & Slatkin, 1976; Meiri et al., 2013; Moreira et al., 2021; but see Labra et al., 2009), we compared the above parameters across species in the four groups (heliotherms, non-heliotherms, diurnal snakes and nocturnal species) using phylogenetic generalized least-square (PGLS) regression in the 'caper' R package (Orme et al., 2013) with  $\lambda$  values selected by maximum likelihood. Models were tested for each response variable ( $T_b$  mean; regression slope, intercept and  $R^2$ ;  $T_b$  skewness) using category (heliotherm, non-heliotherm, snake or nocturnal) and mean annual temperature as predictors (the model for  $T_b$  skewness also included mean  $T_b$  of each species as a fixed factor). We included species-specific body mass (log transformed) and the method of  $T_b$  measurement (see below) as predictors in all models. The height above the ground where air temperature was measured was initially considered but we discarded it because it was not significant and had almost no effect in any model. Body temperature measurement methods included: cloacal temperatures using digital thermocouples and analogue thermometer (193 species, specific thermometer models did not differ from each other), skin temperature using an infrared thermometer (9 species, specific thermometers did not differ from each other) and using a temperature-sensitive radio transmitter (8 species).

### 3 | RESULTS

#### 3.1 | Data summary

We measured the body temperatures of squamates in 25 countries on 6 continents, including tropical, subtropical, temperate, montane, Mediterranean, desert and semi-arid biomes (Figure 1) for a total of 22,543 individuals of 260 species. The full data set is provided in Table S1, and the data descriptors and further explanations necessary to interpret the database are provided in Table 1. We filtered out inactive individuals, species with  $n < 20$  individuals and those without phylogenetic data, leaving 20,231 individual measurements belonging to 210 species representing 25 families (20 to 1207 individuals per species, mean = 96.3, median = 51.5; Figure S1) for the analyses. Of these, substrate temperature ( $T_{sub}$ ) was measured for 14,245 individuals of 176 species. Air temperature ( $T_a$ ) was measured for 19,413 individuals of 198 species. Based on behavioural observations, we defined 138 diurnal lizard species (13,446 individuals) as heliothermic and 35 as non-heliothermic (1955 individuals); we also measured 12 species of diurnal snakes (2695 individuals; note that 12 species is a comparatively small sample size, limiting our conclusions for this group), and 25 nocturnal species (2135 individuals; Figure 2).

#### 3.2 | Species-specific mean temperatures

Mean species  $T_b$  was  $28.3^\circ\text{C} \pm 2.0^\circ\text{C}$  SE (median =  $30.1^\circ\text{C}$ ) and had a strong phylogenetic signal (PGLS: Pagel's  $\lambda = 0.97$ ; 95% CI: 0.88–1.00). Species' mean  $T_b$  ranged from  $7.3^\circ\text{C}$  in the nocturnal diplodactylid gecko *Woodworthia maculata* from New Zealand (the 'Otago/Southland' species of this complex, known for activity in extreme cold  $T_b$ ; Chukwuka et al., 2023), to  $40.1^\circ\text{C}$  in the heliothermic teiid lizard *Cnemidophorus cryptus* from the Amazon. Mean species  $T_{sub}$  was  $26.9^\circ\text{C} \pm 2.1^\circ\text{C}$  (median =  $28.1^\circ\text{C}$ ,  $\lambda = 0.80$ ) ranging from  $8.9^\circ\text{C}$  in *W. maculata* to  $47.7^\circ\text{C}$  in the heliothermic lacertid lizard *Meroles suborbitalis* from South Africa. Mean species  $T_a$  was  $25.2^\circ\text{C} \pm 1.2^\circ\text{C}$  (median =  $26.1^\circ\text{C}$ ,  $\lambda = 0.45$ ) and ranged from  $5.6^\circ\text{C}$  in *W. maculata* to  $33.2^\circ\text{C}$  in the non-heliothermic liolaemid lizard *Phymaturus tenebrosus* from Patagonia. Mean annual temperatures at the measurement site ranged from  $-1.9^\circ\text{C}$  in the heliothermic Andean *Phymaturus antofagastensis* to  $28.8^\circ\text{C}$  in the nocturnal gekkonid gecko *Hemidactylus triedrus* from India.

Mean species  $T_b$  was lower in nocturnal species than in all other categories (Figure 3a). Mean  $T_b$  adjusted for mean  $T_{sub}$  in the PGLS, was higher in heliotherms than in non-heliotherms and nocturnal species ( $p < 0.001$ ). It was moderately correlated with mean  $T_{sub}$  in heliotherms and strongly correlated with mean  $T_{sub}$  in nocturnal and non-heliotherm species ( $\lambda = 0.50$ ;  $R^2 = 0.66$ ; Table 2a; Figure 3b). Mean species  $T_b$  adjusted for mean  $T_a$  was lower in nocturnal species than in heliotherms ( $p < 0.001$ ) and non-heliotherms ( $p = 0.041$ ). It was moderately correlated with mean  $T_a$  in heliotherms, non-heliotherms and diurnal snakes, and strongly correlated with mean  $T_a$  in nocturnal species ( $\lambda = 0.77$ ;  $R^2 = 0.49$ ; Table 2b; Figure 3c). Mean species  $T_b$  was lower in nocturnal species than in all other categories when adjusting for mean annual temperature in the PGLS ( $p < 0.001$  compared to both heliothermic and non-heliothermic diurnal lizards, and  $p = 0.036$  compared to diurnal snakes). Mean  $T_b$  was weakly but significantly positively correlated with mean annual temperature in heliotherms and diurnal snakes, and moderately correlated with mean annual temperature in nocturnal species ( $\lambda = 0.92$ ;  $R^2 = 0.23$ ; Table 2c; Figure 3d). Sensitivity analyses using the Zheng and Wiens (2016) tree provided qualitatively similar results (Appendix S1).

#### 3.3 | Body–environment temperature relationships

##### 3.3.1 | Substrate temperatures

The slopes, intercepts and  $R^2$  values of species'  $T_b$  against  $T_{sub}$  regressions (Table S2) had no phylogenetic signal ( $\lambda = 0$ , both in this analysis and in the sensitivity analysis using the fully resolved tree from Zheng & Wiens, 2016). The slope values of  $T_b$  on  $T_{sub}$  were not different from zero in heliothermic lizards but were positive and significant in all other categories (PGLS:  $R^2 = 0.44$ ; Table 3a; Figure 4a). Intercepts differed from zero in heliotherms ( $28.9^\circ\text{C} \pm 2.0^\circ\text{C}$ ) and non-heliotherms ( $20.1^\circ\text{C} \pm 3.7^\circ\text{C}$ ) but not in diurnal snakes

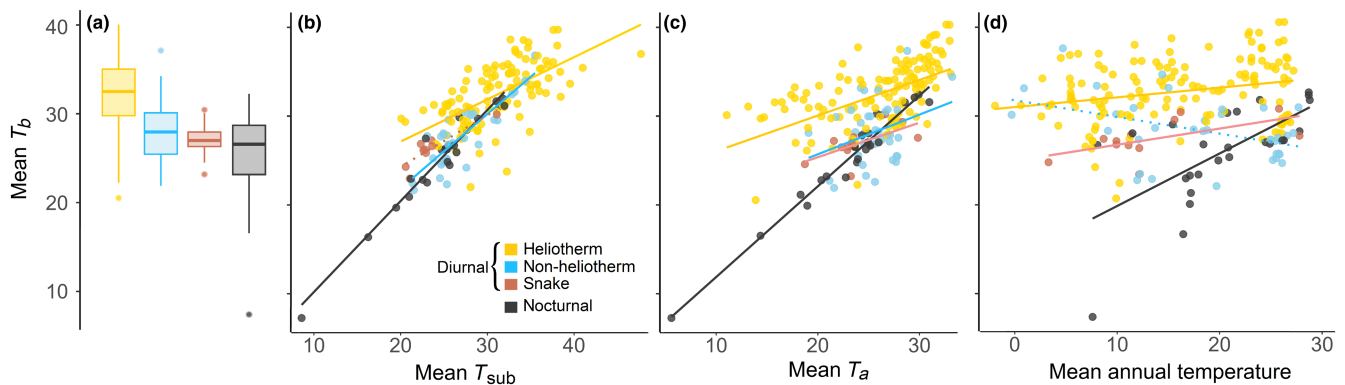
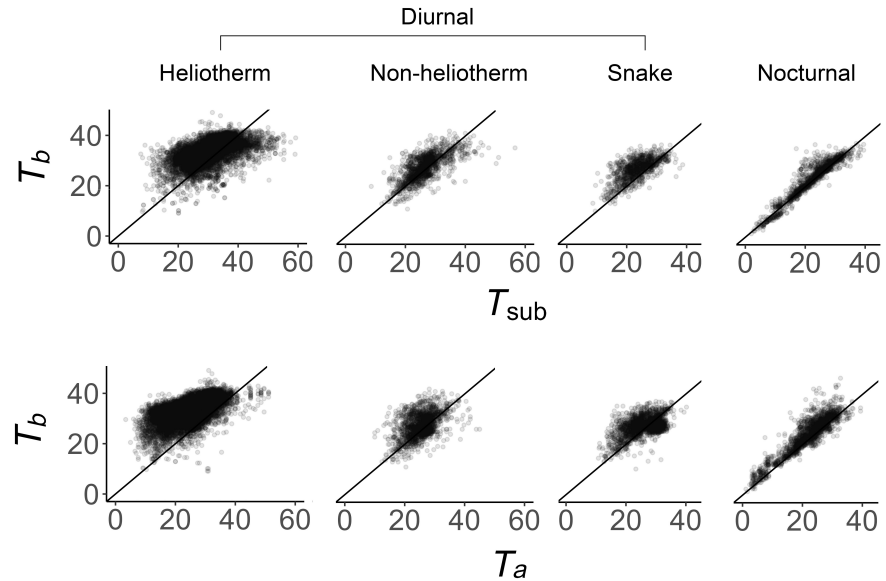
TABLE 1 Details and data description for the database (full data in Table S1).

Column title	Column type	Description
Species	Factor	Binomial name, updated to fit the Reptile Database 2022
Category	Factor	[Based on the data in rows 4–6]. Helio_liz=heliothermic lizard. Non_helio_liz=non-heliothermic lizard. Snake_diur=diurnal snakes. Nocturnal=nocturnal lizards and snakes
Taxon	Factor	Lizard or snake
Activity	Factor	Diurnal or nocturnal. Cathemeral species were assigned to the time of day they had been documented
Behaviour	Factor	Heliothermic or not. According to the literature and the researcher's [see row 12] personal expertise
$T_b$	Integer	Body temperature
$T_{sub}$	Integer	Substrate temperature (at the location where $T_b$ was taken)
$T_a$	Integer	Air temperature (at the location where $T_b$ was taken)
Latitude	Integer	Decimal degrees. If exact location could not be provided (e.g. in protected species where location is not publicly available), rounded to the nearest 0.1 degree
Longitude	Integer	Decimal degrees. If exact location could not be provided (e.g. in protected species where location is not publicly available), rounded to the nearest 0.1 degree
Research group	Factor	Initials of the researchers who measured this individual. People working together and using the same methodology were grouped together
$T_b$ device	Text	Model of the device
$T_b$ method	Factor	$T_b$ device separated into three categories: cloacal probe, skin (infrared) and radio transmitter
$T_a$ device	Text	Model of the device
$T_a$ height	Text	Height of the $T_a$ measurement device above ground
$T_a$ height	Factor	$T_a$ height separated into three categories: <5, 5–15 and >50 cm
Measurement radiation	Text	Was the animal location when caught sunlit, shaded, etc.
$T_{sub}$ device	Text	Model of the device
Country	Factor	Country where the animal was measured (no political statement is intended, in the case of disputed territories)
Date	Text	When the measurement was taken. Exact dates, if known, are in dd/mm/yyyy format
Time	Text	Hour of the measurement, if known
Age	Factor	Adult, subadult, juvenile or unknown
Sex	Factor	Male, female or unknown
Locality	Text	Name of the region or location
Weather	Text	Weather observations at the time of measurement
Log mean sp mass	Integer	$\log_{10}$ of the mean species mass. Mass was calculated from our data if available, or from snout-vent length data using the allometric equations from Feldman et al. (2016) and Meiri et al. (2021)
Notes	Text	Any further information
Active?	Factor	Yes/No. Was the animal active, or not (e.g. sleeping, thermoregulating, resting under cover, etc.)
$T_{sub}$ -use	Factor	Yes/No. Did the data in this row fit the criteria to be used in the $T_{sub}$ analyses ( $n > 20$ active individuals, phylogenetic data present)
$T_a$ -use	Factor	Yes/No. Did the data in this row fit the criteria to be used in the $T_a$ analyses ( $n > 20$ active individuals, phylogenetic data present)

( $12.5^{\circ}\text{C} \pm 6.4^{\circ}\text{C}$ ,  $p=0.052$ ) and nocturnal species ( $7.2^{\circ}\text{C} \pm 5.7^{\circ}\text{C}$ ,  $p=0.210$ ;  $R^2=0.43$ ; Table 3a; Figure 4b). However, heliotherm slopes became steeper with increasing mean annual temperature (Figure 5a), and intercepts became lower (Figure 5b), so that in warmer regions the temperature relations across categories become gradually convergent. Non-heliotherms' slopes were also positively influenced by mean annual temperature ( $p=0.038$ ; Figure 5a), the

effect being similar between them and heliotherms ( $p=0.400$ ), but the relationship between the intercepts and mean annual temperature was not significant ( $p=0.072$ ). The  $R^2$  values for  $T_b$  on  $T_{sub}$  were lowest for heliotherms (0.11), higher for non-heliotherm lizards and diurnal snakes (0.30 and 0.34 respectively) and highest in nocturnal species (0.74; Figure 4c; Table 3). The  $R^2$  values increased with mean annual temperature for heliotherms (model  $R^2=0.45$ ; Table 3a;

**FIGURE 2** Active body temperatures ( $T_b$ ) of the 20,231 individuals used in the analyses, visualized against substrate temperature (top) and air temperatures (bottom). The line represents equality (intercept of 0 and slope of 1). Axis units are degrees Celsius.



**FIGURE 3** Species-specific mean  $T_b$  compared between categories (a) and regressed against (b) mean  $T_{sub}$ , (c) mean  $T_a$  and (d) mean annual temperature. Significant relationships are marked with solid lines. Heliothermic lizard  $T_b$  (yellow) is higher than those of non-heliothermic diurnal lizards (blue), diurnal snakes (red) and nocturnal species (grey) at colder environmental temperatures. Note that non-heliotherm  $T_b$  changes with  $T_{sub}$  similarly to nocturnal species, but changes with  $T_a$  similarly to diurnal species.

Figure 5c). All these results are adjusted for the effects of measuring device and body size (see Section 3.4). Repeating these analyses using the Zheng and Wiens (2016) tree provided qualitatively similar results (Appendix S1).

### 3.3.2 | Air temperatures

The slopes, intercepts and  $R^2$  values of species'  $T_b$  against  $T_a$  regressions (Table S2) had no phylogenetic signal ( $\lambda=0$ , using both trees). The slope values were steeper in nocturnal species compared to both heliotherms (PGLS:  $p=0.002$ ) and non-heliotherms ( $p=0.021$ ), and in diurnal snakes compared to heliotherms ( $p<0.001$ ;  $R^2=0.24$ ; Table 3b; Figure 4d). Intercepts differed from zero in heliotherms ( $26.7^\circ\text{C}\pm 2.1^\circ\text{C}$ ) and non-heliotherms ( $22.8^\circ\text{C}\pm 3.9^\circ\text{C}$ ), and were much lower in diurnal snakes and nocturnal species (1.1 and  $2.5^\circ\text{C}$  respectively; neither being significantly different from zero) compared to both heliotherms ( $p<0.001$ ) and non-heliotherms ( $p<0.005$ ;  $R^2=0.34$ ; Table 3b; Figure 4e). However, both heliotherm

and non-heliotherm intercepts became lower with increasing mean annual temperature (Figure 5e), and slopes of heliotherms became steeper ( $p<0.001$ ; for non-heliotherms,  $p=0.051$ , Figure 5d), so that in warmer regions the temperature relations across categories become gradually convergent. Heliotherms and non-heliotherms did not differ from one another in slope ( $p=0.510$ ) and intercept ( $p=0.323$ ), nor in the effect of mean annual temperature on their slope ( $p=0.672$ ) and intercept ( $p=0.972$ ). The  $R^2$  values were lowest for heliotherms (0.12;  $p<0.001$ ) followed by non-heliotherms (0.16;  $p=0.038$ ), but increased with mean annual temperature only for heliotherms (Figure 5f). For diurnal snakes,  $R^2$  values were higher than for heliotherms ( $p=0.005$ ) and non-heliotherms ( $p=0.018$ ), but decreased with mean annual temperature ( $p=0.039$ ). The  $R^2$  values for nocturnal species (0.81) was higher than for heliotherms ( $p=0.009$ ) and non-heliotherms ( $p=0.034$ ), but not for diurnal snakes ( $p=0.858$ ;  $R^2=0.17$ ; Table 3b; Figure 5f). All these results are adjusted for the effects of measuring device and body size (see Section 3.4). The sensitivity analyses using the Zheng and Wiens (2016) tree provided qualitatively similar results (Appendix S1).



TABLE 2 Main results of the PGLS analyses comparing mean species  $T_b$  across the four categories in relation to (a) mean species  $T_{sub}$ , (b) mean species  $T_a$  and (c) mean annual temperature.

(a)	Mean $T_b$			× Mean $T_{sub}$		
	Estimate	SE	<i>p</i>	Estimate	SE	<i>p</i>
Heliotherm	20.25 <sup>A</sup>	1.57	<0.001	0.384 <sup>A</sup>	0.044	<0.001
Non-heliotherm	7.78 <sup>B,C</sup>	3.28	0.019	0.764 <sup>B,C</sup>	0.118	<0.001
Diurnal snake	15.52 <sup>A,B</sup>	5.80	0.008	0.442 <sup>A,B</sup>	0.242	0.070
Nocturnal	1.59 <sup>C</sup>	2.47	0.521	0.968 <sup>C</sup>	0.093	<0.001
(b)	Mean $T_b$			× Mean $T_a$		
	Estimate	SE	<i>p</i>	Estimate	SE	<i>p</i>
Heliotherm	21.61 <sup>A</sup>	1.59	<0.001	0.319 <sup>A</sup>	0.042	<0.001
Non-heliotherm	15.40 <sup>A</sup>	3.87	<0.001	0.511 <sup>A</sup>	0.146	<0.001
Diurnal snake	11.94 <sup>A,B</sup>	6.04	0.049	0.599 <sup>A,B</sup>	0.233	0.011
Nocturnal	5.98 <sup>B</sup>	2.66	0.026	0.866 <sup>B</sup>	0.101	<0.001
(c)	Mean $T_b$			× Mean annual temp.		
	Estimate	SE	<i>p</i>	Estimate	SE	<i>p</i>
Heliotherm	28.21 <sup>A</sup>	1.92	<0.001	0.125 <sup>A,B</sup>	0.043	0.004
Non-heliotherm	28.86 <sup>A</sup>	2.08	<0.001	-0.001 <sup>B</sup>	0.066	0.984
Diurnal snake	23.67 <sup>A</sup>	3.25	<0.001	0.296 <sup>A,C</sup>	0.129	0.022
Nocturnal	16.07 <sup>B</sup>	2.93	<0.001	0.545 <sup>C</sup>	0.116	<0.001

Note: The left column indicates the model intercept for mean  $T_b$  (i.e. mean  $T_b$  for a species in the category when the predictor temperature is zero) and the right column is its interaction with the predictors. The letters A, B, C indicate significant pairwise differences between categories, whereas *p*-values in bold indicate the difference of the estimate from zero. Values are adjusted for method and body mass.

### 3.3.3 | Partial contributions of substrate and air

The partial  $R^2$  of  $T_{sub}$  was lower in heliothermic lizards (0.07) than in non-heliothermic diurnal lizards (0.18;  $p=0.007$ ) and nocturnal species (0.25;  $p=0.009$ ), but not lower than in diurnal snakes (0.22;  $p=0.248$ ;  $\lambda=0.86$ ;  $R^2=0.22$ ; Figure 6a). Partial  $R^2$  of  $T_a$  was higher in heliotherms (0.15) than in non-heliotherms (0.09;  $p=0.035$ ) but not in diurnal snakes (0.16;  $p=0.303$ ) and nocturnal species (0.15;  $p=0.888$ ;  $\lambda=0.03$ ;  $R^2=0.07$ ; Figure 6b).

### 3.4 | Effect of mass and measurement methods

In all the  $T_{sub}$  models (described in Tables 2b and 3a), the device used for  $T_b$  measurements was a significant factor. Infrared thermometers measured lower  $T_b$  ( $n=9$ ;  $p<0.001$ ), and were associated with regression models with lower intercepts ( $p=0.001$ ), and steeper slopes ( $p=0.038$ ) and  $R^2$  values ( $p=0.001$ ). In the  $T_a$  models (described in Tables 2c and 3b), species measured with radio transmitters had lower  $T_b$  ( $p=0.029$ ) and species measured by infrared thermometers had lower regression intercepts ( $p=0.049$ ). Mass was not significant in the above models. For the model with both  $T_{sub}$  and  $T_a$  as predictors, the partial  $R^2$  of  $T_{sub}$  (corrected for category) was higher by 0.3 when using infrared thermometers compared to the partial  $R^2$  for  $T_{sub}$  using cloacal temperatures ( $p<0.001$ ; Figure S2). We found

no difference in the partial  $R^2$  of  $T_{sub}$  between species measured using radio transmitters and cloacal temperatures ( $p=0.120$ ). The effect of log mass on the partial  $R^2$  of  $T_{sub}$  ( $0.027 \pm 0.036$ ) was non-significant ( $p=0.461$ ). There was no difference in the partial  $R^2$  of  $T_a$  (corrected for category) between infrared thermometers compared to cloacal temperatures ( $p=0.795$ ) but the partial  $R^2$  of  $T_a$  was higher by 0.20 using temperature-sensitive radio transmitters than when measured with cloacal thermometers ( $p=0.006$ ; Figure S2). The effect of log mass on the partial  $R^2$  of  $T_a$  ( $-0.047 \pm 0.025$ ) was non-significant ( $p=0.059$ ).

### 3.5 | The shape of body temperature distributions

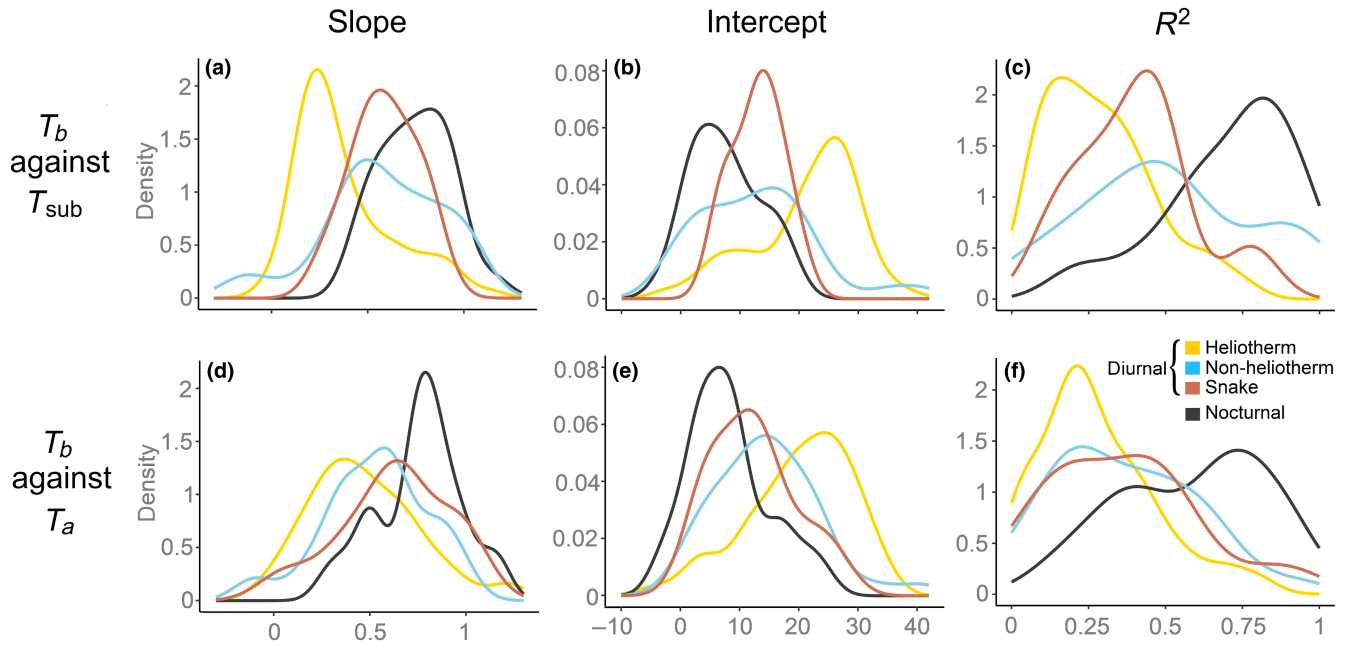
Squamate body temperature distributions were negative (left-skewed) on average (mean:  $-0.39 \pm 0.04$ , median:  $-0.38$ ; calculated using Komsta & Novomestky, 2015). Skewness was negatively correlated with mean  $T_b$  and positively correlated with mean annual temperatures. Thus, distributions were more left-skewed for species with higher body temperatures, especially in colder climates (skewness =  $0.931 - 0.056 \times$  mean  $T_b + 0.027 \times$  mean annual temperature;  $p<0.001$ ;  $\lambda=0.14$ ;  $R^2=0.17$ ; Figure 7). Behavioural category ( $p=0.263$ ), body mass ( $p=0.821$ ) and measurement method ( $p=0.171$ ) were not significantly associated with skewness.

**TABLE 3** Main results of the PGLS analyses comparing the species-specific results (slope, intercept and  $R^2$ ) of  $T_b$  regression against (a)  $T_{sub}$  and (b)  $T_a$  in relation to mean annual temperature at the sites.

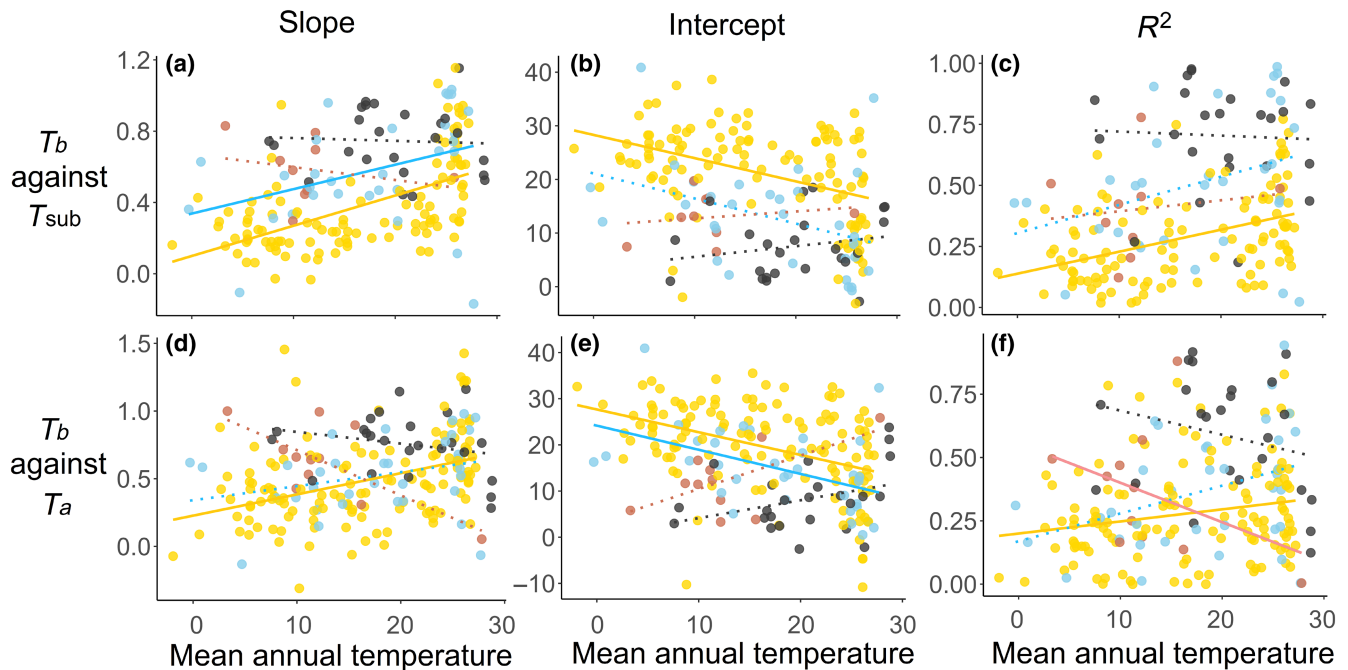
	(a) $T_{sub}$ model				(b) $T_a$ model							
	Slope		× Mean annual temp.		Slope		× Mean annual temp.					
	Estimate	SE	p	Estimate	SE	Estimate	SE	Estimate	SE	p		
Heliotherm	0.048 <sup>A</sup>	0.058	0.409	0.017 <sup>A</sup>	0.002	<0.001	0.212 <sup>A</sup>	0.068	0.002	0.016 <sup>A</sup>	0.003	<0.001
Non-heliotherm	0.314 <sup>B</sup>	0.108	0.004	0.012 <sup>A,B</sup>	0.006	0.038	0.305 <sup>A</sup>	0.131	0.021	0.013 <sup>A,C</sup>	0.006	0.051
Snake	0.569 <sup>B</sup>	0.183	0.002	-0.009 <sup>A,B</sup>	0.013	0.517	0.958 <sup>B</sup>	0.230	<0.001	-0.028 <sup>B,C</sup>	0.015	0.064
Nocturnal	0.692 <sup>B</sup>	0.165	<0.001	<0.001 <sup>B</sup>	0.008	0.983	0.875 <sup>B</sup>	0.209	<0.001	-0.006 <sup>C</sup>	0.010	0.500
	<b>Intercept</b>				<b>Intercept</b>							
	× Mean annual temp.		× Mean annual temp.		× Mean annual temp.		× Mean annual temp.					
	Estimate	SE	p	Estimate	SE	p	Estimate	SE	Estimate	SE	p	
Heliotherm	28.883 <sup>A</sup>	2.008	<0.001	-0.436 <sup>A</sup>	0.087	<0.001	26.674 <sup>A</sup>	2.060	<0.001	-0.493 <sup>A</sup>	0.090	<0.001
Non-heliotherm	20.200 <sup>B</sup>	3.744	<0.001	-0.352 <sup>A</sup>	0.194	0.072	22.799 <sup>A,B</sup>	3.863	<0.001	-0.501 <sup>A</sup>	0.191	0.009
Snake	12.484 <sup>B</sup>	6.370	0.052	0.150 <sup>A</sup>	0.456	0.743	1.122 <sup>B,C</sup>	6.795	0.869	0.741 <sup>B</sup>	0.449	0.101
Nocturnal	7.232 <sup>B</sup>	5.741	0.210	0.075 <sup>A</sup>	0.273	0.783	2.490 <sup>C</sup>	6.304	0.687	0.278 <sup>B</sup>	0.286	0.333
	<b><math>R^2</math></b>				<b><math>R^2</math></b>							
	× Mean annual temp.		× Mean annual temp.		× Mean annual temp.		× Mean annual temp.					
	Estimate	SE	p	Estimate	SE	p	Estimate	SE	Estimate	SE	p	
Heliotherm	0.114 <sup>A</sup>	0.290	<0.001	0.053 <sup>A</sup>	0.012	<0.001	0.123 <sup>A</sup>	0.413	<0.001	0.044 <sup>A</sup>	0.019	0.019
Non-heliotherm	0.342 <sup>B</sup>	0.540	0.228	0.025 <sup>A</sup>	0.028	0.381	0.161 <sup>A</sup>	0.792	0.038	0.056 <sup>A,C</sup>	0.039	0.156
Snake	0.300 <sup>A,B</sup>	0.919	0.357	0.019 <sup>A</sup>	0.066	0.774	0.858 <sup>B</sup>	1.393	0.198	-0.191 <sup>B</sup>	0.092	0.039
Nocturnal	0.737 <sup>B</sup>	0.828	0.215	-0.003 <sup>A</sup>	0.039	0.941	0.813 <sup>B</sup>	1.267	0.247	-0.045 <sup>B,C</sup>	0.059	0.247

\* for logit-transformed  $R^2$  values

Note: The left column of each model indicates the model's estimate for the response factor (i.e. at mean annual temperature = 0) and the right column predicts how the response varies with each °C increase in mean annual temperature. Values are adjusted for methodology and body mass. Pagel's  $\lambda$  was zero for all six models. The letters A, B, C indicate significant pairwise differences between categories, whereas *p*-values in bold indicate the difference of the estimate from zero (equivalent to 0.5 in the logit-transformed values).



**FIGURE 4** Kernel density estimates (smoothed histogram) for the slope (a), intercept (b) and  $R^2$  (c) of the species-specific regressions  $T_b$  against  $T_{sub}$ , and the slope (d), intercept (e) and  $R^2$  (f) of the species-specific regressions  $T_b$  against  $T_a$ . Heliotherms and non-heliotherms show differences in the  $T_{sub}$  models but similarities in the  $T_a$  models. Heliotherms and nocturnal species are very distinct in all parameters, whereas non-heliotherms and diurnal snakes are very similar in all parameters.



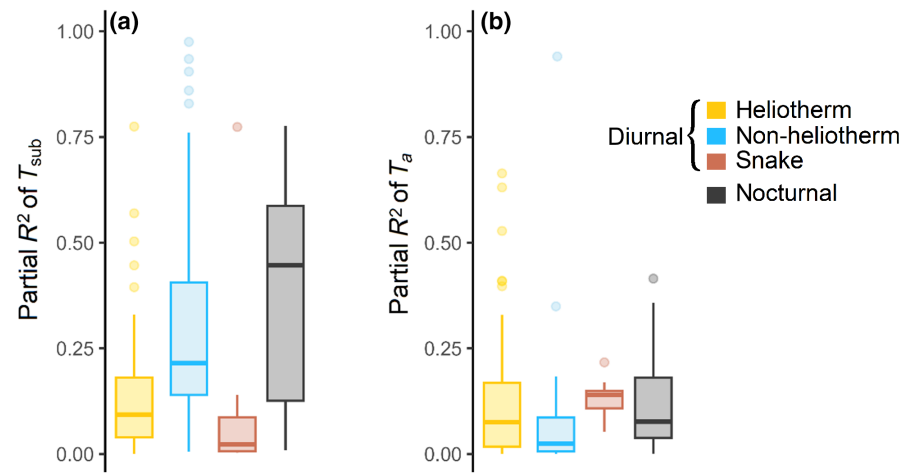
**FIGURE 5** The slope (a), intercept (b) and  $R^2$  (c) of the species-specific regressions  $T_b$  against  $T_{sub}$ , and the slope (d), intercept (e) and  $R^2$  (f) of the species-specific regressions  $T_b$  against  $T_a$ , shown against the mean annual temperature of the sites, with which significant interactions are marked with solid lines. Each point is one species. Heliotherms' and non-heliotherms' regression parameters similarly change with mean annual temperature; thus, the different categories gradually converge as mean annual temperature increases. Heliothermic lizards are shown in yellow, non-heliothermic diurnal lizards in blue, diurnal snakes in red and nocturnal species in black.

#### 4 | DISCUSSION

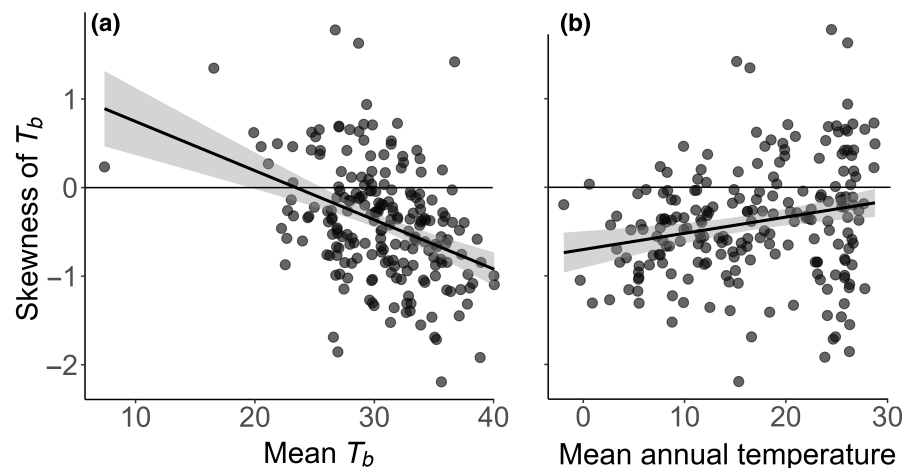
Mean body temperature per species had a very strong phylogenetic signal, which remained high when accounting for the climatic,

behavioural and methodological factors, providing further support that body temperature is a phylogenetically conserved trait (Bogert, 1949; Grigg & Buckley, 2013; Huey & Pianka, 1977; Huey & Slatkin, 1976; Moreira et al., 2021; Moreno Azocar et al., 2013).

**FIGURE 6** Partial  $R^2$  of  $T_{\text{sub}}$  (a) and  $T_a$  (b) as predictors of  $T_b$  in the combined model adjusted for mean annual temperature, measurement method and body mass. Heliotherm partial  $R^2$  is lower than non-heliotherm and nocturnal for  $T_{\text{sub}}$ , but higher than non-heliotherms for  $T_a$ . Substrate temperatures are much more strongly correlated with body temperatures in nocturnal and non-heliothermic species but not in heliotherms or diurnal snakes.



**FIGURE 7** Species-specific mean skewness of  $T_b$  distribution plotted against the species' (a) mean  $T_b$  and (b) mean annual temperature (in °C). Mean  $T_b$  significantly predicts negative skewness, with a weaker opposite effect of mean annual temperature, independently of all other factors tested. Removal of the extreme-cold  $T_b$  outlier does not change the trends.



However, unlike species means, the regression analyses for  $T_b$  in relation to  $T_{\text{sub}}$  and  $T_a$  were phylogenetically independent, but well explained by behavioural and climatic factors (see below). This may be because, while mean  $T_b$  reflects the interplay of preferred and available temperatures (physiological and geographic factors, which may vary from clade to clade), the dependence of  $T_b$  on ambient temperature (for a given behavioural category) reflects biophysical constraints, and is thus less disposed to vary phylogenetically.

#### 4.1 | Body temperature across behavioural categories

The temperature increment gained via radiation (Bakken et al., 1985; Pianka & Huey, 1978; Shine & Kearney, 2001) provides an additional source of heat beyond the equilibrium of conduction and convection with the air and substrate. Heliothermic lizards can achieve higher body temperatures at low ambient temperatures, due to heat from solar exposure (Christian, 1998; Ortega et al., 2016; Valdecantos et al., 2013). This may explain why mean  $T_b$  in diurnal heliotherms in our data set was only slightly lower under cold compared to warm conditions (Figure 3b,c), and their regressions mostly

had high intercepts with shallow slopes approaching zero (Figure 4). By shuttling in and out of shade, heliotherms can also be active at higher  $T_{\text{sub}}$  than is reached by the other groups without overheating. The extra heat source for these species can allow them to be active for longer in the season and grant fitness benefits (Otero et al., 2015), including higher locomotion and digestive efficiency (Huey & Kingsolver, 1989), buffering of embryos or eggs from the cold (Cadby et al., 2014) and better feeding opportunities (Angilletta et al., 2002). The benefits of exposure to radiation (for vitamin D synthesis; Ferguson et al., 2005) may exceed, and sometimes override, thermoregulatory needs (Conley & Lattanzio, 2022).

Mean body temperatures of non-heliothermic diurnal lizards were lower than those of heliotherms but similar to those of nocturnal species and diurnal snakes at similar substrate temperatures. The parameters of  $T_b$  on  $T_{\text{sub}}$  regressions of diurnal non-heliotherms differed from those of heliotherms but resembled those of nocturnal species and diurnal snakes (i.e. steep slopes, low intercepts, high  $R^2$ ). In contrast, their mean  $T_b$  at different air temperatures were similar to those of heliotherms and higher than those of nocturnal species, and their  $T_b$  on  $T_a$  regressions differed from those of nocturnal species but were similar to those of heliotherms (i.e. shallow slopes, high intercepts, low  $R^2$ ). Some of the behaviourally non-heliothermic species may be engaging in thigmothermic thermoregulation (by

conduction with the substrates). The high correlation with the substrate but not the air temperatures raises the possibility that they use warm substrate to heat themselves above cold air. This perhaps explains why when including both temperature indices as predictors of non-heliotherm  $T_b$ , the effect was dominated by  $T_{sub}$  (Figure 6), and why non-heliotherms only occurred across a narrow range of  $T_{sub}$  (Figure 3b; Harvey & Weatherhead, 2010).

While the trends for diurnal lizards generally complied with long-held predictions and expectations from decades of research, diurnal snakes presented an intriguing divergence from these patterns. Snake body temperatures were low compared to heliothermic lizards in nearly all analyses, and the relationship between body temperature and both substrate and air temperatures had steeper slopes and lower intercepts. Diurnal snakes clustered around a small range of mean  $T_b$  and  $T_{sub}$ , possibly due to snakes having narrower thermal preferences (e.g. Harvey & Weatherhead, 2010) which they are able to maintain behaviourally. Due to their elongated, limbless bodies, much of the snake surface area is always in contact with the substrate, with which they can (depending on the substrate) exchange heat to achieve very efficient thermoregulation (Blouin-Demers & Weatherhead, 2001; Lelièvre et al., 2010). This type of thigmothermic thermoregulation might explain the strong relationship between  $T_b$  and  $T_{sub}$  for snakes (Figure 4). Basking snakes may thus absorb heat by conduction from the sun-warmed substrate no less than from the sun directly. Paradoxically, however, snake  $T_b$  against  $T_{sub}$  regressions had low  $R^2$  values. The thermal biology of snakes is not as well-studied as that of lizards, but snakes are considered to generally have lower and more variable  $T_b$  (Avery, 1982; Whitaker & Shine, 2002). However, we cannot rule out some sampling bias—for example, we measured very few hot-climate snake species (see Section 4.5) and did not capture the full range of snake thermal strategies, which may vary widely between species (Lelièvre et al., 2010).

Nocturnal species had consistently lower  $T_b$  compared to heliotherms, both in terms of species means (see Huey & Slatkin, 1976; Moreira et al., 2021; Pianka & Huey, 1978), and lower regression intercepts and steeper slopes (Pianka & Vitt, 2003). Both  $T_{sub}$  and  $T_a$  explained more of the observed variance in body temperatures of nocturnal species than the other groups, suggesting they have fewer thermal opportunities to elevate their body temperature (but see Bertoia et al., 2021; Dial, 1978; Grimm-Seyfarth et al., 2018).

## 4.2 | Body temperature across climates

Mean annual temperature at the location of temperature measurement was positively but weakly correlated with mean  $T_b$  (see also Meiri et al., 2013) for all but the diurnal non-heliotherms for which it had no effect (Figure 3d). Furthermore, in warmer climates the regression slopes of  $T_b$  on  $T_{sub}$  and  $T_a$  were steeper, intercepts lower and  $R^2$  values higher in the diurnal lizards, especially heliotherms (Figure 5). The dependence of the regression parameters on mean annual temperature was very similar between heliotherms and non-heliotherms (but mostly absent in diurnal snakes and nocturnal

species). In cold climates, squamates need to reach performance-enabling body temperatures, and hence need to be able to be warmer than their environment (Anderson et al., 2022; Besson & Cree, 2010; Caldwell et al., 2017; Gómez Alés et al., 2017; Moreno Azocar et al., 2013). This may explain the seemingly opposite trend found by non-phylogenetic studies (Huey et al., 2009), in which mean  $T_b$  actually increased with latitude. Our phylogenetic analysis suggests that this reflects the presence of more non-basking (therefore low  $T_b$ , see Section 4.1) species in the tropics. The shift to weaker statistical relationship of  $T_b$  to  $T_{sub}$  and  $T_a$  in diurnal lizards at colder climates, may stem from the increased need for thermoregulation in cold regions by increased basking (known to occur even in otherwise non-heliothermic species; Hertz & Huey, 1981). This pressure is released in warmer, stable climate (Shine & Madsen, 1996), leading to convergent thermal relationships between the behavioural categories in the tropics. Although nocturnal species' mean  $T_b$  was strongly correlated with mean annual temperature, the correlations—between  $T_b$  and  $T_{sub}$  as well as between  $T_b$  and  $T_a$ —did not change across climate. Even though some nocturnal species can warm themselves on warm surfaces by cryptic thermoregulation (Bertoia et al., 2021; Dial, 1978; Grimm-Seyfarth et al., 2018) or activity early at night (Bustard, 1967; Kearney & Predavec, 2000), it is clearly not enough to keep their  $T_b$  high and stable for long in cold environments. The constraint on nocturnal species, of being active at the colder part of the daily cycle, may have led to adaptations enabling activity at low environmental temperatures, despite the implication of much lower  $T_b$  than a diurnal species would have. The critical thermal minimum is evolutionary labile and is lower in cold environments (Anderson et al., 2022; Moreno Azocar et al., 2013). Cold-climate species often have additional physiological adaptations such as lower preferred  $T_b$  (Labra et al., 2009; Rubalcaba et al., 2023), wider performance curves (Anderson et al., 2022; Bonino et al., 2015; Cruz et al., 2011; but see van Berkum, 1988) and higher metabolic rates (Dubiner et al., 2023; Hare et al., 2010). These adaptations can partially compensate for low  $T_b$ , but limit the environments where nocturnal species can live (Medina et al., 2011; Vidan et al., 2017). Similarly, we found that nocturnal species were active at the lowest  $T_{sub}$  and  $T_a$  (Figure 3b,c) but did not reach the coldest regions (Figure 3d).

## 4.3 | The shape of temperature frequency distributions

Most body temperature distributions were left-skewed (Figure 7) as found for desert lizards by Huey and Pianka (2018). Thus,  $T_b$  during activity is more frequently closer to the maximum than to the minimum temperature limit (i.e. closer to  $CT_{max}$  than to  $CT_{min}$ ). The difference in skewness between species is to a large degree explained simply by mean  $T_b$ , independently of behavioural category or methodology. Temperature distributions of species with higher mean body temperatures were more left skewed, presumably reflecting the fact that the upper thermal limits are similar across species while the lower limits vary more widely (Araújo et al., 2013;



Moreno Azocar et al., 2013). Coupled with the similar left skew of performance curves (Tomlinson, 2019), this distribution leads to a greater portion of activity (integrated over time) to coincide with the thermal optimum for activity (Martin & Huey, 2008). Distributions were more left-skewed at lower mean annual temperatures, either because of individuals active at colder, sub-optimal temperatures in the 'left tail', or because of a higher need for thermoregulatory behaviour in these species (Section 4.2) requiring more careful alignment with the optimal curves.

#### 4.4 | Methodological differences

Cloacal thermometers were much more widely used in our study and generally measured higher temperatures than infrared thermometers. Infrared thermometers were shown to be accurate by some (Chukwuka et al., 2019) and others found them biased (Carretero, 2012), and their suitability may vary across species and conditions. Infrared thermometers measure skin rather than body core temperatures, and the skin is more subjected to direct heat exchange with the substrate than are body core temperatures. Furthermore, in small animals, infrared thermometers may be partly measuring the temperature of the background substrate. Alternatively, animals measured using cloacal thermometers, that needed to be caught by hand, may have warmed up in the act of trying to escape or (though we tried to avoid it) were warmed by the researcher's hands. In snakes, whose bodies are elongate, cloacal  $T_b$  may even differ from the temperature of the head and heart at the front. Future studies across a range of conditions and body sizes are needed to better explain the differences we found.

#### 4.5 | Sampling biases

Some regions harbouring much of the world's squamate diversity, including most of Africa, Asia and the Pacific islands, are strongly underrepresented in our data set. Nocturnal species are also less represented: of our 210 species, 185 species (88%) are diurnal, despite ~40% of squamate species being nocturnal, cathemeral or crepuscular (Shai Meiri, unpublished data for >8200 species). Tropical snakes are only represented in our data by three species, out of the 2655 snake species restricted to the tropics (about 65% of the world's snakes). Thus, our conclusions regarding nocturnal species, and even more so regarding snakes, should be considered preliminary. Sampling biases against these taxa and regions are lamentably common shortfalls in the study of reptile thermal ecology.

#### 4.6 | Additional caveats

The practice of assessing reptile thermoregulation using field data on body and environmental temperatures alone (as we do here) has been criticized (Dreisig, 1984; Heath, 1964; Hertz et al., 1993;

Huey, 1982), mostly due to the incompleteness of air temperatures as a proxy for micro-niche temperature in small animals. Our usage of  $T_{\text{sub}}$  (most reptiles sprawl near the substrate) and body mass in addition to  $T_a$  addresses this in part by accounting for additional components of the thermal environment. That said, the important need for a null model to claim thermoregulation from body–environment relationships has been clear since Heath (1964) demonstrated 'behavioural thermoregulation' in a 'population' of beer cans. Thus, research has largely moved to accompany instantaneous temperature measurements from the field with thermal preference experiments in the laboratory, and the measurement of operative temperatures in animal models over extended times (Shine & Kearney, 2001). Hertz et al. (1993) even went as far as writing that instantaneous field measurements answer an 'inappropriate question'. We acknowledge the importance of these concepts and experiments. Our major focus here was on comparing thermal relations across taxa, behavioural groups and climates, rather than attempting to infer thermoregulatory efficiency, accuracy or precision from the temperature relations themselves. We believe our study design to be robust and our results to be meaningful—even without data on operative temperatures. Measuring instantaneous body and environmental temperatures in the field is straightforward, comparatively inexpensive and provides a wide range of data and large sample sizes across many species. Downstream, this results in a powerful design that can be used to study some of the most essential questions regarding thermal biology. It should not, however, replace the use of more nuanced, and potentially more accurate, use of operative temperature studies and controlled experiments for the direct study of thermoregulation. We heartily encourage our database to also be used together with thermoregulatory information (e.g. modelling the operative temperatures, or factoring in preferred temperatures) as a potential synthesis of macroecological patterns and biophysical thermal ecology.

While a distinction between diurnal and nocturnal species is easy to make (the few cathemeral species in our data set were allocated to the time of day in which measurements were conducted), distinguishing heliotherms from non-heliotherms is sometimes difficult and potentially inaccurate. Species that are often seen basking in direct sunlight were classified as heliotherms. Those that are almost always active under shelter, and virtually never in direct sunlight, were classified as non-heliotherms. We classified less clear-cut cases in this continuum to the best of our ability, according to our knowledge and observations of their behaviour, but we acknowledge that the classification is imperfect. Therefore the 'non-heliotherm' category should be treated with more caution than the other, less ambiguous ones. Future validation, refinement and further interpretation of the patterns presented here, would perhaps benefit from a less subjective categorization of basking strategy (e.g. including habitat traits; Giacometti et al., 2023) and better coverage of squamate lifestyles, habitat types and diversity. Another potential bias in our results could be that squamates were rarely measured at their activity limits. Not many reptiles are active in the field when it is too warm or cold, so we often only study them during peak activity seasons and hours (ours as well as theirs), underrepresenting off-peak times and

cryptic activity in shelters. Hot days and nights may also be under-represented because animals are quicker and, therefore, harder to catch (though reduced shyness at high  $T_b$  may compensate for this; Rand, 1964). This bias is reflected in the occasionally low  $T_b$  values of species we did observe at higher temperatures. Obviously, additional factors not considered herein are known or suspected to influence reptile thermal behaviour and body–environment temperature relationships. Factors such as reproductive status (gravid females are often thought to prefer higher temperatures and bask more often: Blazquez, 1995; Schwarzkopf & Shine, 1991; Werner, 1990; but see Beuchat & Ellner, 1987), and reproductive mode (females of viviparous species may have more stable body temperatures; Cruz et al., 2022; Shine, 2004) are worth considering. Moreover, there may be seasonal changes in thermoregulatory behaviour, thermal tolerance or body temperature (Giacometti et al., 2023; Henle, 1992; Huey & Pianka, 1977), as well as differences related to biomes and substrates. Squamates inhabiting substrates with different thermal properties (trees and rocks of different types, the ground or the subterranean medium, water) are likely to differ in the amount of heat exchanged with the substrate (Sagonas et al., 2017). These properties all lead to testable hypotheses, which can potentially be explored using our data.

## 5 | CONCLUDING REMARKS

Compiling a database of unprecedented magnitude of squamate body temperatures and their environmental correlates allowed us to test hypotheses regarding the thermal characteristics of life in different regions, and of different taxa and behaviour. Overall, the results presented here further our ability to understand how body temperature varies among species and in face of the challenges and opportunities posed by their environments. Moreover, the extensive database we have put together holds much potential for testing a wide variety of questions beyond the scope of the present study, and we encourage its use together with previous compilations of reptile body or environment temperatures and thermal traits.

### AUTHOR CONTRIBUTIONS

S.M. envisioned the study. All authors collected the field data. S.D. designed and performed the analyses and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

All the data necessary to understand and reproduce the results shown in this manuscript are available <https://doi.org/10.5061/dryad.5dv41nscz> and in Table S1 (raw data, see Table 2 for further details and explanations), Table S2 (species-specific results for descriptive statistics and regressions), and Appendix S3 (R code).

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## BIOSKETCH

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## SUPPORTING INFORMATION

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