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RESEARCH ARTICLE

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

Shahar Dubiner[1] | Rocío Aguilar[2,3] | Rodolfo O. Anderson[2] | Diego M. Arenas Moreno[4] | Luciano J. Avila[5] | Estefania Boada-Viteri[6,7] | Martin Castillo[8] | David G. Chapple[2] | Christian O. Chukwuka[9] | Alison Cree[9] | Félix B. Cruz[8] | Guarino R. Colli[10] | Indraneil Das[11] | Michel-Jean Delaugerre[12] | Wei-Guo Du[13] | Angel Dyugmedzhiev[14] | Tiffany M. Doan[15] | Paula Escudero[5] | Jules Farquhar[2] | Alison M. Gainsbury[16] | Brian S. Gray[17] | Annegret Grimm-Seyfarth[18] | Kelly M. Hare[19] | Klaus Henle[18] | Nora Ibargüengoytía[20] | Yuval Itescu[21,22] | Simon Jamison[1] | Octavio Jimenez-Robles[23] | Antonieta Labra[24,25] | Alejandro Laspiur[26] | Tao Liang[27] | Jackie L. Ludgate[9] | Luca Luiselli[28,29] | José Martín[30] | Genevieve Matthews[2] | Marlin Medina[31] | Fausto R. Méndez-de-la-Cruz[4] | Donald B. Miles[32] | Nathan E. Mills[33] | Alejandro Bruno Miranda-Calle[34,35] | Joanne M. Monks[9] | Mariana Morando[5] | Débora L. Moreno Azocar[8] | Gopal Murali[36,37,38] | Panayotis Pafilis[39,40] | Ana Pérez-Cembranos[41] | Valentín Pérez-Mellado[41] | Richard Peters[7] | Ligia Pizzatto[42,43] | Daniel Pincheira-Donoso[44] | Michael V. Plummer[33] | Rachel Schwarz[1] | Ben Shermeister[1] | Richard Shine[45,46] | Ole Theisinger[47] | Wiebke Theisinger[47] | Krystal A. Tolley[48,49] | Omar Torres-Carvajal[6] | Soledad Valdecantos[50] | Raoul Van Damme[51] | Laurie J. Vitt[52] | Erik Wapstra[53] | Geoffrey M. While[53] | Eran Levin[1] | Shai Meiri[1,54]

Correspondence
Shahar Dubiner, School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 6997801, Israel.
Email: dubiner@mail.tau.ac.il

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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

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