

## A worldwide and annotated database of evaporative water loss rates in squamate reptiles

Le Galliard Jean-François <sup>1,2,\*</sup>, Chabaud Chloe <sup>3</sup>, De Andrade Denis Otavio Vieira <sup>4</sup>,  
Brischoux Francois <sup>3</sup>, Carretero Miguel A. <sup>5,6</sup>, Dupoue Andreaz <sup>1,2</sup>, Gavira Rodrigo S. B. <sup>3</sup>,  
Lourdais Olivier <sup>3</sup>, Sannolo Marco <sup>5,7</sup>, Van Dooren Tom J. M. <sup>1</sup>

<sup>1</sup> Sorbonne Univ, iEES Paris, Paris, France.

<sup>2</sup> PSL Res Univ, Ecole Normale Super, Ctr Rech Ecol Expt & Predict CEREEP Ecotron IleDe, Biol, St Pierre Les Nemours, France.

<sup>3</sup> Ctr Etud Biol Chize, Villiers En Bois, France.

<sup>4</sup> Univ Estadual Paulista UNESP, Inst Biociencias, Dept Zool, Rio Claro, Brazil.

<sup>5</sup> Univ Porto, CIBIO Ctr Invest Biodiversidade & Recursos Genet, InBIO, Vairao, Vila Do Conde, Portugal.

<sup>6</sup> Univ Porto, Fac Ciencias, Dept Biol, Porto, Portugal.

<sup>7</sup> CSIC, Museo Nacl Ciencias Nat, Dept Evolutionary Ecol, Madrid, Spain.

\* Corresponding author : Jean-François Le Galliard, email address : [galliard@bio.ens.psl.eu](mailto:galliard@bio.ens.psl.eu)

### Abstract

Motivation The understanding of physiological adaptations, of evolutionary radiations and of ecological responses to global change urges for global, comprehensive databases of the functional traits of extant organisms. The ability to maintain an adequate water balance is a critical functional property influencing the resilience of animal species to climate variation. In terrestrial or semi-terrestrial organisms, total water loss includes a significant contribution from evaporative water loss (EWL). The analysis of geographic and phylogenetic variation in EWL rates must however account for differences in methods and potential confounding factors, which influence standard measures of whole-organism water loss. We compiled the global and standardized SquamEWL database of total, respiratory and cutaneous EWL for 325 species and subspecies of squamate reptiles (793 samples and 2,536 estimates) from across the globe. An extensive set of companion data and annotations associated with the EWL measurements of potential value for future investigation, including metabolic rate data, is provided. We present preliminary descriptive statistics for the compiled data, discuss gaps and biases, and identify promising avenues to update, expand and explore this database.

### Main types of variables contained

Standard water loss rates, geographic data, metabolic rates.

### Spatial location

Global.

---

**Time period**

Data were obtained from extant species and were collected between 1945 and 2020.

**Major taxa**

Reptilia, Squamata including lizards, snakes and amphisbaenians.

**Level of measurements**

Individual samples of animals from the same species, locality, age class and sex category.

**Software format**

CSV.

**Keywords** : ectotherms, evaporative water loss, functional traits, homeostasis, hydroregulation, macrophysiology

## 37 **Acknowledgments**

38 We thank colleagues who helped with data calculation by providing raw or summary data, metadata  
39 or additional information including David Chapple, Allen Cohen, Don Bradshaw, David Chapple,  
40 Pierre-André Crochet, Sebastian Kirchof, Jason Kolbe, Michaël Guillon, Shu-Ping Huang, Jason  
41 Kolbe, Amy MacLeo, Bill Mautz, Francisco Javier Muñoz Nolasco, Anil Oguz, Panayiotis Pafilis,  
42 Catarina Rato, Abderrahim S'khifa, Graham Thompson, Miguel Vences, Philip Withers and  
43 Anamarija Žagar. We thank Luis Miguel Senzano for providing unpublished data. We thank two  
44 anonymous reviewers and Michaël Kearney for comments that helped improve the manuscript.

45

## 46 **Funding**

47 Compilation of the database was funded by the Centre National de la Recherche Scientifique  
48 (CNRS), the Agence Nationale de la Recherche (Aquatherm: ANR-17-CE02-0013 to JFLG) and a  
49 doctoral grant from Ecole normale supérieure to CC.

## 74 **1. Background and summary**

75 The ecological niche of a species is an important concept in correlative species distribution  
76 modeling and describes the multivariate environmental space of abiotic and biotic factors that  
77 determine the boundaries of a species range (Chase & Leibold, 2003). In mechanistic species  
78 distribution models, however, the ecological niche of a species is not inferred from its realized niche  
79 but derived from a calculation of the fundamental niche of the organism, defined as the full range of  
80 conditions and resources suitable for survival and reproduction (Kearney & Porter, 2009). In the last  
81 decade, mechanistic models have become central to uncover the potential effects of global climatic  
82 change on species viability and distribution (Sinervo *et al.*, 2010; Boyle *et al.*, 2020). Since  
83 properties of the fundamental niche are determined by organismal traits, current research aims to  
84 better understand how morphological, physiological and behavioral properties of organisms  
85 constrain their fundamental niche and ultimately define their ecological niche and distribution.

86 The compilation of databases of functional traits, defined as the morphological,  
87 physiological, phenological or behavioral traits that determine the performance of individuals  
88 (Violle *et al.*, 2007; Kearney *et al.*, 2021), is a fundamental step in this research program (Schneider  
89 *et al.*, 2019). Furthermore, global databases of functional traits can be used to investigate universal  
90 scaling rules and advance our understanding of evolutionary processes (Díaz *et al.*, 2016; Etard *et*  
91 *al.*, 2020). Research on the climatic tolerances of ectothermic animals over the last decades has  
92 focused on the study of functional traits characterizing the thermal biology, including thermal limits  
93 (Sunday *et al.*, 2012; Bennett *et al.*, 2018), thermal performance curves and metabolism (Dillon *et*  
94 *al.*, 2010), thermoregulation behavior (Kearney *et al.*, 2009), or thermal sensitivity of development  
95 (Noble *et al.*, 2018). However, studies have shown that traits associated with water balance in  
96 ectotherms are also critical in setting their climatic niche, their sensitivity to global changes, and  
97 their macro-evolutionary radiation patterns (Brischoux *et al.*, 2012; Kearney *et al.*, 2018; Garcia-

98 Porta *et al.*, 2019; Gouveia *et al.*, 2019; Rozen-Rechels *et al.*, 2019; Lertzman-Lepofsky *et al.*,  
99 2020).

100 In animals, water balance is dynamically regulated by the constant adjustments of water loss  
101 and water intake processes (Figure 1A) which depend on morphological features and physiological  
102 and behavioral mechanisms (e.g., behavioral hydroregulation, skin resistance to water loss or  
103 respiration, Chown *et al.*, 2011; Pintor *et al.*, 2016; Pirtle *et al.*, 2019; Riddell *et al.*, 2019). As a  
104 result, body hydration state is homeostatically maintained within a safety zone by compensating  
105 water loss with input from metabolic, food and drinking water to avoid the acute and chronic,  
106 potentially lethal, effects of dehydration. Total evaporative loss (TEWL) comprises both the water  
107 lost through the skin epidermis or exoskeleton (cutaneous water loss, CWL) and via the respiratory  
108 system (respiratory water loss, RWL). Although functional traits such as desiccation resistance and  
109 behavioral traits are also important for hydroregulation, the standard rate of EWL has proven to be a  
110 relevant metric to assess water regulation strategies, and to scale the susceptibility of organisms to  
111 drought, habitat aridity or salinity in birds (Albright *et al.*, 2017; Boyle *et al.*, 2020), mammals (Van  
112 Sant *et al.*, 2012), non-avian reptiles (Brischoux *et al.*, 2012; Cox & Cox, 2015), amphibians  
113 (Lertzman-Lepofsky *et al.*, 2020) and insects (Addo-Bediako *et al.*, 2001). However, to our  
114 knowledge, there has been no attempt to compile and annotate a global database of all published  
115 EWL records in terrestrial animals, including those of squamate reptiles.

116 Squamate reptiles share proximate mechanisms of water loss (Mautz, 1982). They are ideal  
117 model systems to study the relevance of water regulation strategies under a macroecological  
118 mechanistic approach since these dry-skinned ectothermic organisms exhibit great phylogenetic and  
119 ecological diversification, broad variation in body size and shape, and are found in most habitats  
120 across the globe (Meiri, 2018). In addition, their performance and life history strategies are greatly  
121 influenced by the availability of water in their environment (Kearney & Porter, 2004; Lillywhite,  
122 2017; Rozen-Rechels *et al.*, 2020). Rates of TEWL vary with micro-climatic conditions,

123 morphological and functional adaptations, life stages and behavioral strategies (e.g., space use and  
124 activity, Pirtle *et al.*, 2019). In squamates, EWL is not as tightly associated with body temperature  
125 regulation as in endothermic animals. Indeed, heat loss due to CWL and RWL, i.e., evaporative  
126 cooling, is generally negligible in squamate reptiles, except under extreme conditions such as  
127 panting in some desert species or under extreme heat stress (Tattersall *et al.*, 2006; Loughran &  
128 Wolf, 2020). Although CWL is generally the dominant avenue of water loss in squamate reptiles,  
129 the partitioning between RWL and CWL, which includes trans-epidermal, ocular and cloacal water  
130 loss, varies between and within species (Mautz, 1982; Pirtle *et al.*, 2019). One important factor  
131 affecting the partitioning between CWL and RWL is body size, which is largely determined by the  
132 fact that surface area and skin thickness (the primary determinants of CWL) scale differently with  
133 body size than respiration rate and lung size (primary determinants of RWL, Mautz, 1980, 1982) do.  
134 Changes in patterns and rates of EWL can rapidly evolve in squamates, and there is evidence of  
135 adaptive plastic responses of TEWL to fluctuating temperatures or hydric conditions (Kattan &  
136 Lillywhite, 1989; Moen *et al.*, 2005; Cox & Cox, 2015; Garcia-Porta *et al.*, 2019; Sannolo *et al.*,  
137 2020). Yet, estimates of TEWL are influenced by methodological choices, sampling methods (e.g.,  
138 size class or seasonal factors), acclimation procedures and statistical reporting methods, which  
139 makes comparisons across studies difficult without an unambiguously defined vocabulary and a  
140 broad set of standardized metadata (see Figure 1B).

141         Here, we assembled a global and annotated database of rates of evaporative water loss in  
142 squamate reptiles of the world using published information and unpublished data we collected in  
143 recent years. Our initiative differs from previously published data sets by (1) its broad taxonomic  
144 scope spanning all available data for all squamate reptiles including lizards, snakes and  
145 amphisbaenians, (2) its exhaustiveness since we gathered all identified published estimates from a  
146 pre-established list of acceptable methodologies and recorded samples and units from the original  
147 publications without *a priori* exclusion of particular data or *ad hoc* calculations of statistics, and (3)

148 its comprehensiveness since we compiled information on 30 metadata variables. We provide a  
149 computing script to facilitate future use of these data. Whenever available, we recovered and report  
150 all the variables necessary for the calculation of skin resistance to evaporation  $R_s$ , a functional trait  
151 relevant to the predictive modeling of water-flow balance (Kearney *et al.*, 2021) and of central  
152 relevance in mechanistic niche distribution models (Riddell *et al.*, 2017). We also compiled a  
153 second companion database on metabolic rate ( $VO_2$  and  $VCO_2$ ) for those cases in which this  
154 information was also available on the same source material examined for the construction of the  
155 EWL database. We judge this companion database relevant under the primary goal of this paper,  
156 since it may ease future studies focusing on the partitioning between CWL and RWL (Gates, 1980;  
157 Pirtle *et al.*, 2019).

158         We make the compiled database freely available to stimulate future research on water  
159 balance in reptiles, particularly on water conservation mechanisms and even more so on the  
160 geographic, ecological, and phylogenetic correlates of evaporative water loss. We expect to  
161 encourage other researchers to work on the expansion of the database and consult it to identify  
162 understudied groups and which set of variables are relevant to be measured and reported. Finally,  
163 we hope that our database will be useful for those willing to use it to construct mechanistic niche  
164 models (Kearney & Porter, 2020)

## 165 **2. Methods and dataset**

166 We searched for published literature and referenced reports providing potential data on water loss  
167 rates in squamate reptiles in Web of Science and Google Scholar using relevant search terms in title,  
168 abstract and content with the following query: (“water loss” OR “water balance” OR  
169 ”hydroregulation”) AND (“reptile\*” OR “snake\*” OR “lizard\*” OR “squamate\*”). In addition, we  
170 extracted all references from a recent comparative analysis of water loss in reptiles (Cox & Cox,  
171 2015). The availability of water loss data on samples of individuals (excluding eggs or embryos)

172 from known reptile species was then checked by a single person (JFLG) who stored all such  
173 references, source files as well as available online data in a Zotero group library (see  
174 <https://tinyurl.com/y2nclru5>). Using tags, all publications were then assigned to a single person who  
175 oversaw confirming availability of water loss data, extracting the data and adding relevant metadata  
176 to a spreadsheet. If additional relevant publications were identified, those were added to the Zotero  
177 library and processed by the same individual. This procedure was performed first in September  
178 2018 and repeated in October 2019, February 2020, and September 2020 and spans data sources  
179 published from 1932 to late 2020. Additionally, unpublished data were also contributed by our  
180 research group. In March 2021, we added metadata following up on review requests, extracted  
181 additional information on metabolism and validated the database again.

182         We produced a library of 160 publications, reports or academic contributions (monographs,  
183 dissertations and theses) from which we extracted complete or partial data (see PRISMA workflow  
184 in Supplementary File 1). EWL data were then added into a spreadsheet together with all the  
185 available metadata describing the relevant conditions of water loss measurements, species and  
186 sample characteristics, and contextual information regarding animal morphology, location, sampling  
187 dates and habitat. The species and subspecies identities were standardized using the EMBL/EBI  
188 Reptile DataBase release of December 21, 2019 (Uetz & Etzold, 1996). We performed data  
189 extraction accepting a sample data point as defined by a unique group of animals composed of a  
190 fixed set of individuals, subjected to the same experimental protocol, and measured under the same  
191 conditions. For each sample, we extracted the mean and dispersion statistics (SD, SE or range) of  
192 EWL rates (total water loss, respiratory water loss or cutaneous water loss) and the mean and  
193 dispersion statistics (SD, SE, or range) of body mass as well as mean statistics for body size (snout  
194 to vent and total length) and body surface area. Data were taken from published or shared datasets,  
195 extracted from tables and text, or extracted from figures using scanned images of the plots and the  
196 Plot Digitizer program in Java (<https://sourceforge.net/projects/plotdigitizer/>). Information on



197 measurement method, temperature (air, skin surface and core body temperature), water vapor  
198 pressure deficit (VPD) in the air, air flow, measurement duration, and activity statuses of animals  
199 were extracted whenever available or requested from the corresponding authors. We added  
200 additional information on chamber characteristics and average diameter of the chambers to make it  
201 possible to calculate air velocity from air flow. All data is presented as values on the scales chosen  
202 for reporting, although, whenever possible, the possibility for scale conversion is provided (see  
203 below). These metadata were selected because they provide important contextual information about  
204 dominant factors of methodological variation in measurements of EWL (Mautz, 1980).

205         A mechanistic understanding of water balance requires a careful quantification of the  
206 functional traits governing variation in CWL and RWL among species and the use of biophysical  
207 models of EWL (Gates, 1980; Kearney & Porter, 2009; Pirtle *et al.*, 2019). In RWL, water is lost by  
208 evaporation from the lung respiratory surface to air contained in it at a rate determined by the water  
209 vapor density gradient. The establishment of the water vapor density gradient, in turn, depends on  
210 the relative humidity and temperature of the inhaled air and the pace at which the air inside the  
211 lungs is renewed, i.e., total ventilation (Gates, 1980). Total ventilation is determined by a  
212 combination of breathing frequency and tidal volume and is linked to the adequate match of  
213 metabolic demand (Pirtle *et al.*, 2019). Thus, RWL should increase monotonically with air  
214 temperature, air dryness, body temperature, and increased metabolic activity. CWL is mostly  
215 determined by the water vapor gradient between the skin surface and the air, which is established by  
216 the interaction of air temperature and relative humidity, air convection rate, an animal's shape and  
217 size, both affecting skin surface area, and, finally, the intrinsic resistance of the skin to evaporative  
218 water loss or  $R_s$  (Gates, 1980; Mautz, 1980). Thus, from a functional standpoint,  $R_s$  informs on a  
219 central organismal determinant of the animal's susceptibility to lose water via evaporation being,  
220 possibly, the best standardized metric to compare samples, populations and species (Gates, 1980;  
221 Pirtle *et al.*, 2019). Several studies have quantified and compared  $R_s$  among closely related

222 squamate reptile species (Dmi'el, 1998, 2001; Oufiero & Van Sant, 2018), but accurate values of  $R_s$   
223 are generally unavailable for most species to date (Mautz, 1982). Therefore, for those cases in  
224 which the information could be recovered, we collected and reported all the components necessary  
225 for calculating  $R_s$ , even though we have not added it as a singled-out variable in the dataset  
226 (Kearney & Porter, 2020). Note that there are potential caveats with respect to this approach  
227 because of unknowns in the regional variation of skin and body temperatures (Barroso *et al.*, 2016),  
228 difficulties to partition sub-components of EWL (Senzano & Andrade, 2018), and further study or  
229 species-specific features (Mautz, 1982).

230         We also included variables describing study design (groups and treatments) and a quality  
231 score permitting the exclusion of data (abnormal animals, animals maintained under manipulated  
232 conditions or measurements performed in non-standard conditions) in future extraction and  
233 analysis. Each of us scored a study data quality ranging from high (appropriate protocols, protocols  
234 are well reported, and data statistics are detailed), medium (one item is missing) to low (poorly  
235 designed, poorly reported protocols and poorly detailed data statistics). The same person also scored  
236 the data standards as either usable to not usable data (because of low study standards or  
237 inappropriate metadata, see detailed comments available in a free text item). The content of the  
238 database is outlined in Table 1, which provides additional information on each field of the data  
239 table. Upon data extraction, each record was checked by the data collectors and the content and  
240 integrity of the whole database was checked by two individuals prior to uploading the first version,  
241 called SquamEWL, in a public repository available at DOI: 10.5281/zenodo.3666172 (Le Galliard  
242 *et al.*, 2020). Routines for data extraction, database integrity check and data cleaning were coded in  
243 the R statistical language, and are briefly described below. The fully annotated code written for R  
244 version 3.6.3 (R Core Team, 2020) is also available in the public repository and includes functions  
245 to convert records between measurement scales.

### 246 **3. Preliminary analyses**

247 The SquamEWL dataset includes 2536 water loss records of 325 species and sub-species (301  
248 unique species) of squamate reptiles for 793 unique samples (mean number of individuals per  
249 sample =  $10.15 \pm 11.5$  SD, median = 6, range=1-169) with most measurements obtained for TEWL  
250 (N = 2146) and substantially fewer for CWL (264) and RWL (126). The vast majority of records is  
251 from field-captured animals (N = 2015) in comparison to laboratory acclimated animals or those  
252 raised in outdoor enclosures (N = 203). There is substantial variation in the acclimation time of  
253 animals (time spent in the laboratory prior to measurement), even after excluding laboratory-raised  
254 animals (range=0-750 days, mean =  $46.45 \pm 119.4$  SD, median = 7). The predominant protocol  
255 involves measurements of body mass loss in the laboratory (N = 1391), followed by direct  
256 measurements of water vapor changes in flow-through chambers (N = 760), measurements of the  
257 mass increase of a desiccant (N = 296), doubly-labeled water techniques in active animals (N = 56)  
258 and, in more recent studies, flux chamber protocols for measurements of trans-epidermal water loss  
259 (N = 33). The variation in micro-climatic environmental conditions during sampling is wide with air  
260 temperatures ranging from 5.3 to 45°C (mean =  $28 \pm 6.47$  SD, median = 27), VPD in the air ranging  
261 from ca. zero to 9.10 kPa (mean =  $2.83 \pm 1.73$  SD, median = 2.53) and air flow ranging from zero to  
262 several hundred mL per min (mean =  $146.5 \pm 267.8$  SD, about half of the records were obtained in  
263 still air).

264         The geographic origin is available for 1923 records comprising 316 unique localities (Figure  
265 2A) predominantly located in Northern and Central America, Europe and Australia, with under-  
266 representation in pan-tropical diversity hotspots including South America, Africa and Asia as well  
267 as several semi-arid and arid regions of Africa, the Arabian Peninsula and remaining Asia sub-  
268 tropical regions (Roll *et al.*, 2017). The altitudinal range varied from sea level up to 3,718 m above  
269 sea level with most records below 500 m (mean = 367.7 m, median = 74 m), which reflects the

270 prevalent altitudinal range for Squamata (Buckley *et al.*, 2008, 2012). The dataset contains  
271 representatives of 34 families but only 2.71 % of the total species richness estimated for squamates.  
272 Given the contribution of different families to the total species richness of squamate reptiles  
273 worldwide (Uetz & Etzold, 1996; Roll *et al.*, 2017), there is an “over-representation” of species  
274 from Lacertidae, Phrynosomatidae, Teiidae, Diplodactylidae, Sphaerodactylidae and Viperidae and  
275 an “under-representation” of species from Gekkonidae, Gymnophthalmidae, Elapidae, Scincidae  
276 and Colubridae (Figure 2B).

277 In addition to heterogeneity in sampling, measurements conditions and laboratory methods,  
278 calculations of water loss rates vary among studies. In particular, EWL rates are reported on three  
279 different scales, namely as mass-relative values (% of initial body mass or mg per g per hour, 1544  
280 records), absolute values (mg water per hour, 715 records), or surface-relative values (mg per cm<sup>2</sup>  
281 per hour, 270 records). To convert all EWL records to a single scale (mg per hour), we gathered  
282 records reported for the same samples under the same conditions on different scales and used a  
283 statistical procedure to fit a calibration function to convert data from relative to absolute scale (see  
284 Supplementary File 1). Using this approach, we calculated 1884 unique estimates of absolute EWL  
285 rates, including TEWL, CWL and RWL components. Preliminary non-phylogenetic analyses  
286 indicated that TEWL and CWL rates scale allometrically with body mass with an exponent of ca.  
287 0.6-0.7 (linear regression on a log-log scale, TEWL: slope =  $0.66 \pm 0.0154$  SE, CWL: slope =  $0.59$   
288  $\pm 0.048$  SE; see Figure 2C), which is close to the 2/3 allometric exponent for the geometric  
289 increment of surface area with the increment in body mass. The RWL component is generally  
290 smaller than CWL component of TEWL in small-sized species and increases faster with body mass  
291 (linear regression on a log-log scale, RWL: slope =  $0.88 \pm 0.058$  SE), as expected from the 3/4  
292 allometric exponent relating ventilation and metabolic rates to body mass. After correction for body  
293 mass but not for experimental conditions, records of TEWL showed no clear altitudinal cline across  
294 all samples (linear regression with log-transformed WL and mass,  $F_{1,959} = 0.56$ ,  $P = 0.09$ ), but a

295 small negative latitudinal cline (linear regression with log-transformed WL and mass,  $F_{1,960} = 5.25$ ,  $P$   
296  $= 0.02$ ). Future analyses should explore more in depth the effects of species characteristics and  
297 environmental conditions (e.g., temperature and humidity, habitat aridity) on inter-specific variation  
298 in EWL.

299 Physical equations of TEWL require additional information on the temperature of the  
300 animals, the body shape and air velocity, and the metabolism (see above). Surface ( $N = 90$ ) and  
301 body ( $N = 190$ ) temperatures were very rarely reported because they are usually difficult to measure  
302 and it is often assumed that they are at equilibrium with air temperature, which is not true in general  
303 (Warburg, 1965). Air velocity could be calculated for most records ( $N = 2204$ ) and ranged from  
304 zero to 0.017 m per second (mean  $= 0.0014 \pm 0.0029$  SD). We extracted 394 usable metabolic data  
305 values from the same sources as in SquamEWL database including 105 unique species and  
306 subspecies from 184 samples, which we present in a separate companion dataset. Notwithstanding  
307 that, we provide the necessary functions to merge these data with those of the SquamEWL for users  
308 potentially interested in mechanistic modeling of CWL and RWL using the NicheMapR software  
309 (Pirtle *et al.*, 2019).

#### 310 **4. Conclusion and perspectives**

311 The present dataset greatly expands previous compilations of EWL in squamate reptiles by nearly  
312 doubling the number of species (ca. 100 species in Mautz, 1982; 139 species in Cox & Cox, 2015)  
313 It also provides exhaustive metadata about methods, contexts and protocols in which each unique  
314 data point was obtained. This expanded and fully annotated dataset will ease transparent and  
315 reproducible statistical manipulation of EWL data for future studies, allow to examine how much  
316 variation in EWL is caused by methodological factors instead of ecological or evolutionary drivers,  
317 facilitate the estimation of skin resistance for an expanded list of species and will therefore ease  
318 comparative analyses of EWL. The dataset may also assist in estimates of TEWL, CWL and RWL,

319 the conversion between different measurement scales and the identification of records performed  
320 within pre-defined set of conditions such as standard records with non-manipulated animals at rest.  
321 This is particularly important given the substantial differences in methodology among studies and  
322 the inherent variability in EWL values caused by air temperature, air humidity and air velocity  
323 during measurements. Potential case studies will include methodological analyses of microclimatic  
324 factors such as temperature and humidity, partitioning of intra- and inter-specific variation and  
325 comparative phylogenetic analyses of the diversification and environmental constraints on EWL  
326 across species.

327         Despite earlier suggestions to better standardize EWL measurement protocols (Mautz,  
328 1982), the current data covers a broad range of methods and contexts, and we found it difficult to  
329 suggest an optimal and unique way to measure EWL in squamate reptiles because the exact protocol  
330 will always depend on the specific research questions. Obviously, broad-scale comparisons of EWL  
331 in poorly explored taxa and geographic areas would benefit from the use of simple approaches  
332 where water loss is measured with a gravimetric method on animals at rest during a few hours in  
333 controlled conditions in a ventilated box (Garcia-Porta *et al.*, 2019). On the other hand, functional  
334 studies will require detailed quantification of the processes and patterns of water loss and therefore  
335 continuous-time gas measurements following standard guidelines on animals at rest in controlled  
336 conditions in flow-through chambers (Lighton, 2018).

337         We hope that the compiled metadata information of our database (see Figure 1B) will foster  
338 the improvement of data reporting standards. In particular, we recommend that future studies of  
339 EWL in squamate reptiles report systematically details of animal origin, husbandry conditions  
340 before measurements, protocols and measurements conditions, and provide central tendencies and  
341 dispersion statistics on absolute scales (mg per hour) or supply the raw data. We also hope to  
342 stimulate future researchers to collect and report all the variables necessary to quantify skin  
343 resistance to water loss  $R_s$ , a potentially central metric to mechanistic modeling approaches (Riddell

344 *et al.*, 2017). For example, macro-ecological studies may focus on spatial analyses of how climatic  
345 and other abiotic aspects of the habitat interact to determine species distributions and their  
346 vulnerability to environmental disturbances.

347 Our dataset further identifies critical geographic and taxonomic gaps that may be valuable in  
348 guiding future investigations. The limited geographic and poor taxonomic coverage of our dataset  
349 reflect known gaps in herpetological and ecological research (Roll *et al.*, 2017; Meiri, 2018; Etard  
350 *et al.*, 2020). Such gaps and biases are also not surprising for functional traits related to physiology  
351 for which coverage is much lower than ecological, life history, and morphological traits (> 20%  
352 species coverage according to Etard *et al.*, 2020). Given that the water balance physiology of  
353 squamate reptiles has been far less investigated than their thermal biology, we sustain that it is  
354 crucial that a gap-filling effort be directed to the sampling of more data in undersampled areas and  
355 taxonomic groups. More specifically, we shall mention the scarcity of data for Gekkonidae,  
356 Scincidae and Colubridae on a taxonomical basis, and, from areas in South America, Africa and  
357 Asia. The database will be regularly updated with these new data to provide a central resource for  
358 ecological and evolutionary research on this particular animal group.

### 359 **Data Accessibility**

360 Data are available on the Global Ecology and Biogeography webpage and on Zenodo (doi:  
361 10.5281/zenodo.3666172).

### 362 **References**

- Addo-Bediako, A., Chown, S.L. & Gaston, K.J. (2001) Revisiting water loss in insects: a large scale view. *Journal of Insect Physiology*, **47**, 1377–1388.
- Albright, T.P., Mutiibwa, D., Gerson, A.R., Smith, E.K., Talbot, W.A., O’Neill, J.J., McKechnie, A.E. & Wolf, B.O. (2017) Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences*, **114**, 2283–2288.

- Barroso, F.M., Carretero, M.A., Silva, F. & Sannolo, M. (2016) Assessing the reliability of thermography to infer internal body temperatures of lizards. *Journal of Thermal Biology*, **62**, 90–96.
- Bennett, J.M., Calosi, P., Clusella-Trullas, S., Martínez, B., Sunday, J., Algar, A.C., Araújo, M.B., Hawkins, B.A., Keith, S., Kühn, I., Rahbek, C., Rodríguez, L., Singer, A., Villalobos, F., Olalla-Tárraga, M.Á. & Morales-Castilla, I. (2018) GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Scientific Data*, **5**, 180022.
- Boyle, W.A., Shogren, E.H. & Brawn, J.D. (2020) Hygric Niches for Tropical Endotherms. *Trends in Ecology & Evolution*, S0169534720301737.
- Brischoux, F., Tingley, R., Shine, R. & Lillywhite, H.B. (2012) Salinity influences the distribution of marine snakes: implications for evolutionary transitions to marine life. *Ecography*, **35**, 994–1003.
- Buckley, L.B., Hurlbert, A.H. & Jetz, W. (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, **21**, 873–885.
- Buckley, L.B., Rodda, G.H. & Jetz, W. (2008) Thermal and energetic constraints on ectotherm abundance: a global test using lizards. *Ecology*, **89**, 48–55.
- Chase, J.M. & Leibold, M.A. (2003) *Ecological niches: linking classical and contemporary approaches*, University of Chicago Press.
- Chown, S.L., Sorensen, J.G. & Terblanche, J.S. (2011) Water loss in insects: An environmental change perspective. *Journal of Insect Physiology*, **57**, 1070–1084.
- Cox, C.L. & Cox, R.M. (2015) Evolutionary shifts in habitat aridity predict evaporative water loss across squamate reptiles. *Evolution*, **69**, 2507–2516.
- Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D. & Gorné, L.D. (2016) The global spectrum of plant form and function. *Nature*, **529**, 167–171.
- Dillon, M.E., Wang, G. & Huey, R.B. (2010) Global metabolic impacts of recent climate warming. *Nature*, **467**, 704-U88.



- Dmi'el, R. (2001) Skin resistance to evaporative water loss in reptiles: a physiological adaptive mechanism to environmental stress or a phyletically dictated trait? *Israel Journal of Zoology*, **47**, 56–67.
- Dmi'el, R. (1998) Skin resistance to evaporative water loss in viperid snakes: habitat aridity versus taxonomic status. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, **121**, 1–5.
- Etard, A., Morrill, S. & Newbold, T. (2020) Global gaps in trait data for terrestrial vertebrates. *Global Ecology and Biogeography*, **29**, 2143–2158.
- Garcia-Porta, J., Irisarri, I., Kirchner, M., Rodríguez, A., Kirchhof, S., Brown, J.L., MacLeod, A., Turner, A.P., Ahmadzadeh, F., Albaladejo, G., Crnobrnja-Isailovic, J., De la Riva, I., Fawzi, A., Galán, P., Göçmen, B., Harris, D.J., Jiménez-Robles, O., Joger, U., Jovanović Glavaš, O., Kariş, M., Koziel, G., Künzel, S., Lyra, M., Miles, D., Nogales, M., Oğuz, M.A., Pafilis, P., Rancilhac, L., Rodríguez, N., Rodríguez Concepción, B., Sanchez, E., Salvi, D., Slimani, T., S'khifa, A., Qashqaei, A.T., Žagar, A., Lemmon, A., Moriarty Lemmon, E., Carretero, M.A., Carranza, S., Philippe, H., Sinervo, B., Müller, J., Vences, M. & Wollenberg Valero, K.C. (2019) Environmental temperatures shape thermal physiology as well as diversification and genome-wide substitution rates in lizards. *Nature Communications*, **10**, 4077.
- Gates, D.M. (1980) *Biophysical ecology*, Springer-Verlag, New York, USA.
- Gouveia, S.F., Bovo, R.P., Rubalcaba, J.G., Silva, F.R.D., Maciel, N.M., Andrade, D.V. & Martinez, P.A. (2019) Biophysical Modeling of Water Economy Can Explain Geographic Gradient of Body Size in Anurans. *The American Naturalist*, **193**, 51–58.
- Kattan, G.H. & Lillywhite, H.B. (1989) Humidity acclimation and skin permeability in the lizard *Anolis carolinensis*. *Physiological Zoology*, **62**, 593–606.
- Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350.
- Kearney, M. & Porter, W.P. (2004) Mapping the fundamental niche: Physiology, climate, and the distribution of a nocturnal lizard. *Ecology*, **85**, 3119–3131.
- Kearney, M., Shine, R. & Porter, W.P. (2009) The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences*, **106**, 3835–3840.
- Kearney, M.R., Jusup, M., McGeoch, M.A., Kooijman, S.A.L.M. & Chown, S.L. (2021) Where do functional traits come from? The role of theory and models. *Functional Ecology*, **n/a**.

- Kearney, M.R., Munns, S.L., Moore, D., Malishev, M. & Bull, C.M. (2018) Field tests of a general ectotherm niche model show how water can limit lizard activity and distribution. *Ecological Monographs*.
- Kearney, M.R. & Porter, W.P. (2020) NicheMapR – an R package for biophysical modelling: the ectotherm and Dynamic Energy Budget models. *Ecography*, **43**, 85–96.
- Le Galliard, J.-F., Chabaud, C., de Andrade, D.O.V., Brischoux, F., Carretero, M.A., Dupoué, A., Gavira, R., Lourdais, O., Sannolo, M. & van Dooren, T.J.M. (2020) SquamEWL: A worldwide and annotated database of evaporative water loss rates in squamate reptiles.
- Lertzman-Lepofsky, G.F., Kissel, A.M., Sinervo, B. & Palen, W.J. (2020) Water loss and temperature interact to compound amphibian vulnerability to climate change. *Global Change Biology*, **26**, 4868–4879.
- Lighton, J.R.B. (2018) *Measuring Metabolic Rates: A Manual for Scientists*, Second Edition. Oxford University Press, Oxford, New York.
- Lillywhite, H.B. (2017) Feeding begets drinking: insights from intermittent feeding in snakes. *Journal of Experimental Biology*, **220**, 3565–3570.
- Loughran, C.L. & Wolf, B.O. (2020) The functional significance of panting as a mechanism of thermoregulation and its relationship to the critical thermal maxima in lizards. *Journal of Experimental Biology*, **223**.
- Mautz, W.J. (1980) Factors influencing evaporative water loss in lizards. *Comparative Biochemistry and Physiology Part A*, **67A**, 429–437.
- Mautz, W.J. (1982) *Patterns of evaporative water loss. Biology of the Reptilia* (ed. by C. Gans) and F.H. Pough), pp. 443–481. Academic Press, London.
- Meiri, S. (2018) Traits of lizards of the world: Variation around a successful evolutionary design. *Global Ecology and Biogeography*, **27**, 1168–1172.
- Moen, D.S., Winne, C.T. & Reed, R.N. (2005) Habitat-mediated shifts and plasticity in the evaporative water loss rates of two congeneric pit vipers (Squamata, Viperidae, *Agkistrodon*). *Evolutionary Ecology Research*, **7**, 759–766.
- Noble, D.W.A., Stenhouse, V., Riley, J.L., Warner, D.A., While, G.M., Du, W.-G., Uller, T. & Schwanz, L.E. (2018) A comprehensive database of thermal developmental plasticity in reptiles. *Scientific Data*, **5**, 180138.
- Oufiero, C.E. & Van Sant, M.J. (2018) Variation and repeatability of cutaneous water loss and skin resistance in relation to temperature and diel variation in the lizard *Sceloporus consobrinus*. *Journal of Comparative Physiology B*, **188**, 671–681.

- Pintor, A.F.V., Schwarzkopf, L. & Krockenberger, A.K. (2016) Hydroregulation in a tropical dry-skinned ectotherm. *Oecologia*, **182**, 925–931.
- Pirtle, E.I., Tracy, C.R. & Kearney, M.R. (2019) *Hydroregulation. Behavior of Lizards: Evolutionary and Mechanistic Perspectives* (ed. by V. Bels) and A.P. Russell), pp. 343–374. CRC Press (Taylor & Francis Group), Boca Raton, Florida, USA.
- R Core Team (2020) *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria.
- Riddell, E.A., Apanovitch, E.K., Odom, J.P. & Sears, M.W. (2017) Physical calculations of resistance to water loss improve predictions of species range models. *Ecological Monographs*, **87**, 21–33.
- Riddell, E.A., Iknayan, K.J., Wolf, B.O., Sinervo, B. & Beissinger, S.R. (2019) Cooling requirements fueled the collapse of a desert bird community from climate change. *Proceedings of the National Academy of Sciences*, **116**, 21609–21615.
- Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G.R., Dabool, L., Das, I., Doan, T.M., Grismer, L.L., Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., Lewin, A., Martins, M., Maza, E., Meirte, D., Nagy, Z.T., de C Nogueira, C., Pauwels, O.S.G., Pincheira-Donoso, D., Powney, G.D., Sindaco, R., Tallowin, O.J.S., Torres-Carvajal, O., Trape, J.-F., Vidan, E., Uetz, P., Wagner, P., Wang, Y., Orme, C.D.L., Grenyer, R. & Meiri, S. (2017) The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology & Evolution*, **1**, 1677–1682.
- Rozen-Rechels, D., Badiane, A., Agostini, S., Meylan, S. & Le Galliard, J.-F. (2020) Water restriction induces behavioral fight but impairs thermoregulation in a dry-skinned ectotherm. *Oikos*, **129**, 572–584.
- Rozen-Rechels, D., Dupoué, A., Lourdais, O., Chamailé-Jammes, S., Meylan, S., Clobert, J. & Galliard, J.-F.L. (2019) When water interacts with temperature: Ecological and evolutionary implications of thermo-hydroregulation in terrestrial ectotherms. *Ecology and Evolution*, **9**, 10029–10043.
- Sannolo, M., Civantos, E., Martín, J. & Carretero, M.A. (2020) Variation in field body temperature and total evaporative water loss along an environmental gradient in a diurnal ectotherm. *Journal of Zoology*, **310**, 221–231.

- Schneider, F.D., Fichtmueller, D., Gossner, M.M., Güntsch, A., Jochum, M., König-Ries, B., Provost, G.L., Manning, P., Ostrowski, A., Penone, C. & Simons, N.K. (2019) Towards an ecological trait-data standard. *Methods in Ecology and Evolution*, **10**, 2006–2019.
- Senzano, L.M. & Andrade, D.V. (2018) Temperature and dehydration effects on metabolism, water uptake and the partitioning between respiratory and cutaneous evaporative water loss in a terrestrial toad. *Journal of Experimental Biology*, **221**, jeb188482.
- Sinervo, B., Mendez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Cruz, M.V.S., Lara-Resendiz, R., Martinez-Mendez, N., Calderon-Espinosa, M.L., Meza-Lazaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepulveda, P.V., Rocha, C.F.D., Ibarguengoytia, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J. & Sites, J.W. (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science*, **328**, 894–899.
- Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686–690.
- Tattersall, G.J., Cadena, V. & Skinner, M.C. (2006) Respiratory cooling and thermoregulatory coupling in reptiles. *Respiratory Physiology & Neurobiology*, **154**, 302–318.
- Trabucco, A. & Zomer, R. (2019) Global Aridity Index and Potential Evapotranspiration (ET0) Climate Database v2.
- Uetz, P. & Etzold, T. (1996) The EMBL/EBI Reptile Database. *Herpetological Review*, **27**, 174–175.
- Van Sant, M.J., Oufiero, C.E., Muñoz-Garcia, A., Hammond, K.A. & Williams, J.B. (2012) A phylogenetic approach to total evaporative water loss in mammals. *Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches*, **85**, 526–532.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.
- Warburg, M.R. (1965) The influence of ambient temperature and humidity on the body temperature and water loss from two Australian lizards, *Tiliqua rugosa* (Gray) (Scincidae) and *Amphibolurus barbatus* cuvier (Agamidae). *Australian Journal of Zoology*, **13**, 331–350.
- Zheng, Y. & Wiens, J.J. (2016) Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Molecular Phylogenetics and Evolution*, **94**, 537–547.

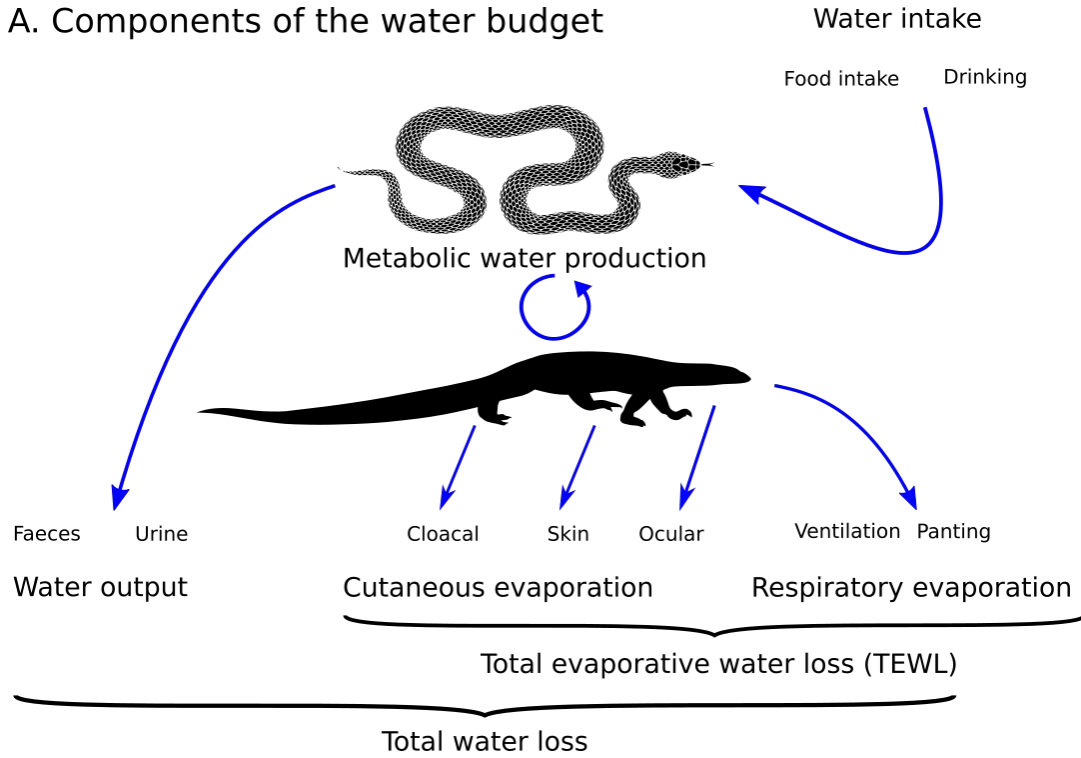
## 363 **Figure legends**

364 **Figure 1.** Components of water loss in squamate reptiles and metadata required to describe evaporative  
365 water loss (EWL). A. The total water budget of the animal rests on balance between water intake from food  
366 and drinking of rain, free standing water or moisture, metabolic water production and water loss from  
367 respiratory evaporation (RWL), water loss from skin, ocular or cloacal evaporation (CWL) and water loss  
368 from feces and excreta. Total evaporative water loss (TEWL) is the sum of total respiratory and cutaneous  
369 evaporative water loss and can be measured from post-absorptive animals in controlled laboratory conditions  
370 provided they do not produce feces or excreta. B. Controlled description of EWL rates data using metadata  
371 describing properties of entities (observations, including species, population and animals), observations  
372 (including characteristics, protocols and context) and values. A rich metadata set is especially needed to  
373 describe the methodology and the environmental conditions when EWL was measured. Each concept in this  
374 figure refers to one or several columns of metadata in our database (see Table 1 for details). The database  
375 was linked with associated data on metabolic rate (MR) whenever the study reported concurrent estimates of  
376 MR for the same animals.

377 **Figure 2.** A. Geographic distribution of data records with exact coordinates of sampling location when  
378 available. The geographic location of data records is mapped over a raster map of the Global Aridity Index  
379 (GAI) for the 1970-2000 period (Trabucco & Zomer, 2019). The aridity index represents the ratio between  
380 rainfall and a measure of potential evapo-transpiration (hyper-arid:  $GAI < 0.03$ ; arid:  $GAI < 0.2$ ; semi-arid:  
381  $0.2 < GAI < 0.5$ ; dry sub-humid:  $0.5 < GAI < 0.65$ ; humid:  $GAI > 0.65$ ; the scale includes a larger range of  
382 humid conditions for the sake of visualization). B. Phylogenetic tree of the Squamata according to a recent  
383 time-calibrated phylogeny by (Zheng & Wiens, 2016). We calculated the proportion of species sampled  
384 (black portion of each barplot) according to the Reptile Database (Uetz & Etzold, 1996) and the total number  
385 of records for each family. Data deficient families are highlighted in blue. C. Allometric scaling of water loss  
386 rates (mg water loss per hour) with body mass in 1485 records across 305 species for which TEWL, total  
387 CWL and total RWL could be calculated. All individual data points are displayed on a log-log scale together  
388 with the best linear non-phylogenetic regression line for each EWL component.

389  
390  
391  
392  
393  
394  
395  
396  
397  
398  
399  
400  
401

A. Components of the water budget



B. Controlled description of EWL

